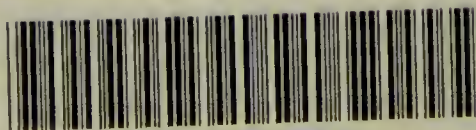




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# The House Fly

*Musca domestica*, Linnæus

A Study of its Structure, Development,  
Bionomics and Economy

BY

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## PREFACE.

The appearance of a volume of this form needs, I feel, some explanation. When first I expressed the intention of publishing the results of my study of the House-fly in parts as they were completed, it was suggested to me that, as the separate parts of the monograph would appear at different times and therefore in different volumes of the *Quarterly Journal of Microscopical Science*, a useful purpose would be served if, on the completion of the work, I were to have the separate parts bound and published in volume form. Such is my apology for the appearance of what, obviously, is by no means a perfect production from a publisher's standpoint. Sir Ray Lankester, K.C.B., the Editor of the *Q.J.M.S.*, kindly allowed me to obtain two hundred copies of the letterpress and plates of each part, the three parts appearing in 1907, 1908 and 1909 respectively. The number of copies of this edition of the monograph is, therefore, very limited. The Manchester University Press has been good enough to undertake the re-publication of these reprints in a volume, and has given me an opportunity of adding some fresh introductory matter as well as appendices giving additional facts and a *résumé* of such work as did not strictly come within the scope of the monograph; there are also included certain matters of practical importance. My thanks are due to the Press Committee for overlooking the clumsiness of the form in its wish to make my work more accessible to students of the subject. In view of the foregoing facts I feel that my readers will pardon the defects of appearance, such as the numbering of the figures, etc., which are the inherent drawbacks of the parts not being immediately consecutive to each other at the time of their original

appearance. For the sake of reference an index has been prepared and a separate pagination has been given above the original pagination, which was retained for the sake of the cross references in the text of the separate parts. The original numbering of the plates has been retained, and as the plates of each part are to be found immediately following that part no difficulty should be experienced in referring to the figures.

This work was carried out while I was a member of the Zoological Staff of the Manchester University, and I should like again to express my sincere thanks to my former teacher, Prof. Sydney J. Hickson, and to the Council of the University for the opportunities which they gave me for the prosecution of my studies. I would also take this opportunity of thanking Sir Ray Lankester for his help in the matter of publication.

C. GORDON HEWITT.

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## INTRODUCTION.

“Familiarity breeds contempt.” This, until a few years ago, was certainly the case with regard to man’s attitude towards the house-fly, and it not infrequently happens that some animals are so common that they are not considered of sufficient scientific interest to be worthy of study. It is unfortunately too often considered by zoologists, probably unknowingly, that the ultimate value of the careful study of an animal is directly proportionate to its rarity. A little reflection will afford other instances of the neglect of common creatures.

Of all animals associated with man, none is more common; he has no attendant more constant. Wherever he has travelled the ‘domestic’ fly has accompanied him, by water and by land; whether he travels on the modern ocean liner, on the Canadian Pacific trans-continental express making its three thousand miles journey, or in the humble electric car from street to street, house-flies are his constant companions.

Recent investigations, however, have shown that we must substitute “fear” for “contempt” in the old adage in the case of this ubiquitous companion. The house-fly is not “a wholesome little creature” as it was described by one whose scientific knowledge is as profound as it is accurate (I refer to an editorial published in a well-known and much-advertised English journal commenting on a lecture that was delivered by me a few years ago on the dangers of the house-fly), but it is an animal which normally bears on its feet, legs and body and leaves in its tracks the organisms productive of decay and not infrequently disease. This is

the animal which not only constantly dines with us, tests the wholesomeness of our food and of the food of our children, but also regales its palate with the juices of the excremental products of various animals, including man. Constant in its attendance upon us in our sleep—which is often disturbed—and when awake, we are apt to lose sight of that side of the fly's life, of its double life, which is passed out of doors, most frequently in search of a place to deposit its eggs, which is equivalent to saying in search of excrement or decaying vegetable substances.

It has been tried and found guilty in spite of the questionings of those who maintain the doctrine that every creature performs some useful purpose. Undoubtedly the fly does, for where there is an abundance of filth, there will the flies gather together, there will they multiply and increase. Its function to-day is nothing more or less than a danger signal to indicate insanitary conditions and the presence in the neighbourhood of decaying or excremental substances. Abolish these and the breeding places of the flies will be eradicated; maintain them and this potential disease carrier will be retained within our houses.

The importance of the house-fly as a disease carrier is considered at length in the third part of this monograph and in Appendix A., and I have considered briefly the preventive and remedial measures in Appendix C. It will never become a rare insect, and the vision of my friend Sir James Crichton Browne of the aged person showing the wondering child the only specimen existing of the house-fly in the British Museum will, unfortunately, never be realised; but there is no reason why, by the adoption of such sanitary measures as the breeding habits of the insect have indicated to be necessary, it should not be considerably decreased in numbers and rendered impotent as a disease carrier. We need such determination and zeal on the part of public bodies as that displayed by the New York

Merchants' Association to abate this dangerous insect in our midst. The subjection of the house-fly is as possible as that of mosquito, compared with which it is equally dangerous and far more so in populated areas. A complete study of the life-history of the larvæ and of the breeding habits of the fly has given the key to the methods of prevention and remedy. The solution of the evil has been given; it remains only for medical officers of health and those in whose hands the health and well-being of the people is entrusted to apply these results. Sufficient words of advice and warning have been spoken, action is needed.

C. GORDON HEWITT.

OTTAWA,  
*January, 1910.*



# The House Fly



# The Structure, Development, and Bionomics of the House-fly, *Musca domestica*, Linn.

## Part I.—The Anatomy of the Fly.

By

**C. Gordon Hewitt, M.Sc.,**

Lecturer in Economic Zoology, University of Manchester.

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With Plates 22—26.

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### I. INTRODUCTION.

THIS paper is intended to be the first of a series of three dealing with the anatomy, development and bionomics of the House-fly, *Musca domestica*, L. The second part will

include an account of the anatomy of the larva, its development and the breeding habits of the fly; the series will be concluded with an account of the bionomics of the fly with special reference to its relations with man.

The term "House-fly" to the zoologist refers only to one insect—*Musca domestica* of Linnæus, but to the popular mind it includes insects, not different species only, but different families of *Diptera*. The Root Maggot fly (Pl. 22, fig. 2), *Anthomyia radicum*, L., sometimes occurs commonly in houses. *Homalomyia canicularis*, L. (fig. 3), often called the Small House-fly, is a very common inhabitant of houses. The latter species is smaller than *M. domestica*, and on this account they are frequently supposed to be young specimens of the latter species by persons who are ignorant of the fact that growth takes place during the larval stage and not after the exclusion of the imago. *Stomoxys calcitrans*, L. (fig. 4), is found in houses, especially in the autumn. It is frequently mistaken for *M. domestica*, and as it is one of the blood-sucking species (See Austen, 1906), the pernicious habit is attributed to the harmless *M. domestica* either on account of the supposed ill-nature of the latter or the influence of some change in the weather.<sup>1</sup>

In addition to these, other species of flies occur in houses but these will be considered in a later part. Reference has been made here to the various species inhabiting houses to show that the term "House-fly" as ordinarily used is rather an inclusive one.

The House-fly has received some attention from naturalists in all ages. Reaumur (1738), De Geer (1752-78) and Bouche (1834) have all included a short account of this insect in their classical memoirs. They do not contribute much to our knowledge of the anatomy and development of the fly. The

<sup>1</sup> *Stomoxys calcitrans* can be readily distinguished from *M. domestica* by the awl-like proboscis which projects forwards from beneath the head. It has a more robust general appearance, a dark spotted abdomen, and its flight is more steady.



most complete of these early accounts is that of Keller (1790) which is illustrated by several striking plates. He gives an interesting account of the development and breeding habits, but in attempting to describe the anatomy he was not so successful as exemplified by his mistaking the brown testes for kidneys. In 1874 Packard wrote what is up to the present time the most complete account of the development of this species, and in 1880 Taschenburg, in his 'Praktische Insektenkunde' gave a good popular account of the insect. Howard has more recently (1898 and 1902) contributed to our knowledge of the developmental history.

No complete account of the anatomy of this insect has yet been published. A short popular account by Samuelson and Hicks (1860) though interesting is very superficial, and contains much that is inaccurate. Macloskie (1880) has published an account of the proboscis of *M. domestica*, and the foot has been made an object of study by several workers, chief of whom are Hepworth (1854), and Merlin (1895 and 1905), who correctly described the glandular hairs of the pulvilli. Wesche has recently (1906) described the genitalia of both sexes, but his description and figures are inaccurate. An interesting account of the copulation of the fly has been published by Belese (1902), in which he briefly describes the reproductive organs, his work will be referred to later. Lowne's monograph (1895) on the Blow-fly (*Calliphora erythrocephala*), which is an elaboration of his previous memoir (1870) is the only complete account which has been published on Muscid anatomy. The result of my study of the anatomy of *M. domestica*, which was begun in 1905, and is being continued in the Zoological Laboratories of the Manchester University, has been to make it apparent that much of Lowne's work needs confirmation.

*Musca domestica* was first described by Linnæus (1758), his description is as follows:—

"Antennis plumatis pilosa nigra, thorace lineis 5 obsoletis abdomine nitidulo tessellato: minor. Habitat in Europæ

domibus, etiam Americæ. Larvæ in sino equinæ. Pupæ parallele cubantes."

Later Fabricius described it more fully in his 'Genera Insectorum.' The House-fly, together with the Blowfly, and the blood-sucking flies *Stomoxys* and *Glossina* belongs to the family *Muscidæ*, which is characterised by having the terminal joint of the antenna—the arista always combed or plumed and by the absence of large bristles or macrochætæ on the abdomen. The *Muscidæ*, together with the *Anthomyidæ* and *Tachinidæ* constitute the group *Muscidæ acalypteratæ* are characterised by the possession of squamæ, small lobes at the bases of the wings which cover the halteres. In the *acalyptate* muscids the squamæ are absent or rudimentary. These two groups belong to the suborder *Cyclorhapha*, one of the two primary divisions of the *Diptera*. The *Cyclorhapha* have coarctate pupæ, the pupal case being formed by the hardening of the last larval skin, and the flies escaping through a circular orifice formed by the fly pushing off the end of the pupa by means of an inflated sac-like organ—the ptilinum which is afterwards withdrawn into the head, its presence being marked by a frontal crescentic opening the lunule. The other sub-order the *Orthorrhapha* have obtected pupæ.

The most complete specific description of *Musca domestica* has been given by Schiner (1864), of which the following is a free translation :—

"Frons of male occupying a fourth part of the breadth of the head. Frontal stripe of female narrow in front, so broad behind that it entirely fills up the width of the frons. The dorsal region of the thorax dusty grey in colour with four equally broad longitudinal stripes. Scutellum grey, with black sides. The light regions of the abdomen yellowish, transparent, the darkest parts at least at the base of the ventral side yellow. The last segment and a dorsal line blackish brown. Seen from behind and against the light the whole abdomen shimmering yellow, and only on each side of the dorsal line on each segment a dull transverse band. The

lower part of the face silky yellow, shot with blackish brown. Median stripe velvety black. Antennæ brown. Palpi black. Legs blackish brown. Wings tinged with pale grey with yellowish base. The female has a broad velvety black, often reddishly shimmering frontal stripe, which is not broader at the anterior end than the bases of the antennæ, but becomes so very much broader above that the light dustiness of the sides is entirely obliterated. The abdomen gradually becoming darker. The shimmering areas on the separate segments generally brownish. All the other parts are the same as in the male."

The mature insects measure from 6-7 mm. in length and 13-15 mm. across the wings. Flies which have been starved during the larval stage or subjected to adverse conditions are generally smaller in size.

## II. METHODS.

All the details of the anatomy which are about to be described have been studied by means of dissections. The dissections were made on both fresh and preserved material under a Ziess' binocular dissecting microscope with magnifications varying from 25-65 diameters. Serial sections have been made to confirm the dissections and to study the histological details.

Perfect series of sections of the whole fly were hard to obtain on account of the somewhat brittle nature of the internal chitinous structures. These internal chitinous skeletal elements caused the greatest trouble as they were apt to damage the internal anatomy. Celloidin sections were not a great improvement on those cut in paraffin. The best results were obtained by fixing the flies from 12-24 hours in Henning's solution, which is—Nitric acid 16 parts, chromic acid (.5 per cent.) 16 parts, corrosive sublimate saturated in 60 per cent. alcohol 24 parts, picric acid saturated in water 12 parts, and absolute alcohol 42 parts, washing out with iodine alcohol. This not only fixes, but to a certain extent, though not completely, softens the chitin. They should not

be imbedded too long or the chitin becomes brittle again. Serial sections made of recently emerged imagines before the chitin has hardened give good results. Other fixing agents used were Perenyi, Rabl's Chromoformic, Picro-formal (Boum's solution), Glacial acetic acid, and absolute alcohol. Of the various stains which were used the most satisfactory were Heidenhain's Iron-hæmatoxylin, Brazilin,<sup>1</sup> and Delafield's Hæmatoxylin. With the last stain perfect results were obtained by overstaining and differentiating with acid-alcohol.

The structure of the thoracic ganglion was studied by means of reconstructions. The method employed was as follows:—The sections were drawn by means of the camera lucida on Bristol board of a thickness proportional to the magnification. They were afterwards cut out and scccotined together. The resulting model was trimmed and soaked in melted paraffin, taken out and dipped several times till a thin coating of paraffin covered the model. This was then trimmed down to the original size, all the interstices having been filled by the paraffin. After a coating of graphite it was electrotyped with copper. In this way a permanent model was obtained.

### III. EXTERNAL STRUCTURE.

#### 1. The Head Capsule.

The head capsule of *M. domestica* presents great modifications when compared with the typical insect head. Considerable difficulty is experienced in explaining its structure in the morphological terms employed in the simpler orders of insects. Lowne did not lessen the difficulty in describing the head of the blowfly by the invention of new terms of little morphological value. The head of the fly is strongly convex in front (Pl. 23, fig. 1), the posterior surface being almost flat and slightly conical. For the sake of clearness the

<sup>1</sup> See Hickson, S. J., "Staining with Brazilin," 'Quart. Journ. Mier. Sci.,' vol. 44, pp. 469—471, 1901.

composition of the head capsule will be described from behind forwards. The occipital foramen occupies a median slightly ventral position on the posterior surface. It is surrounded by the occipital ring, the inner margin of which projects into the cavity of the head. From the sides of the inner margin of the occipital ring two short chitinous bars bend inwards and approach each other internally, forming a support—the jugum for the tentorial membrane. On each side of the occipital ring below the jugum a small cavity occurs into which a corresponding process from the prothorax fits, forming a support for the head.

The occipital ring is surrounded by the four plates, which make up the sides and back of the head capsule. On the ventral side, between the occipital ring and the aperture from which the proboscis depends, a median basal plate, the gulo-mental plate, represents the fused gula and basal portions of the greatly modified second maxillæ. The occipital segment is bounded laterally by the genæ (Lowne's paracephala) and dorsally by the epicranium. These parts have been divided by systematists into so many regions that a somewhat detailed description will be necessary to make their boundaries clear.

The genæ bear the large compound eyes which occupy almost the whole of the antero-lateral regions of the head. On the posterior flattened surface of the head the genæ are flat, and extend from the gulo-mental plate to the epicranial plate, the sutures of the latter being vertical. On the dorsal side each sends a narrow strip between the inner margin of the eye and the epicranium; this strip surrounds the eye and meets the ventral portion of the gena; it is of a silver to golden metallic lustre. On the ventral side below the eye each gena bounds the proboscis aperture laterally; a number of stout bristles arise from this margin and also from its antero-lateral region, which is often spoken of as the "jowl." In the anterior region, where the genæ are in contact with the clypeus, there are two prominent ridges bearing strong setæ; these are usually known as the "facialia."



The epicranium (epicephalon of Lowne) on the posterior surface of the head is flat. On the anterior surface it is convex, and divided into a number of regions. On the top of the head between the eyes it is called the vertex. This contains the three ocelli situated on a slightly raised ocellar triangle, which is surrounded by a second triangle, the vertical triangle. The median region in front of and below the vertex is the frons. In the middle of this there is a black frontal stripe. In the male the eyes are only narrowly separated by the frontal stripe. In the female the frontal stripe widens out on the vertex. This character provides a ready means of distinguishing the male from the female, as the result of it is that in the male the eyes are close together on the dorsal side being separated by about one fifth of the width of the head, whereas in the female the space between the eyes is about one third the width of the head. The edges of the genæ bordering on the frons bear each a row of stout setæ—the fronto-orbital bristles. The antennæ arise from the lower edge of the frons. Each antennæ consists of three joints and the arista. The two proximal joints are short and compose the "scape." The third joint, the flagellum, is longer, somewhat cylindrically prismatic in shape, and hangs vertically in front of the clypeus. It is covered with sensory setæ, and contains two pits of sensory function (olfactory, I believe). From the upper side the plumose arista arises. This probably represents the terminal three joints of the antenna. The lower edge of the frons represents the anterior margin of the epicranium.

The rest of the facial region is composed of the clypeus or, as it is usually called, the face—a convenient term, but one which hides its true morphology. The face is depressed, and is covered by the flagellæ of the antennæ. Between the upper and lateral edges of the face and the lower edge of the epicranium a crescentic opening, the lunule, marks the invagination of the ptilinum. The epistomium is a narrow strip below the face bounding the anterior edge of the proboscis aperture.

The Skeleton of the Proboscis.—The proboscis of *M. domestica* is very similar to that of the blowfly, which has been described by Kraepelin (1880) and Lowne (1895), though the results of these authors differ in many details. My study of *M. domestica* confirms Kraepelin's results, and as Lowne's is the only complete account of the muscid head a full description of its internal and external anatomy will be given in this paper.

Lowne regards the greater part of the proboscis as being developed from the first maxillæ and not from the labium or fused second maxillæ, which is the usually accepted view and one which I support on morphological grounds. On account of his exceptional conclusion he refuted the commonly accepted terms for the various parts and invented new ones. It will be necessary for the sake of descriptive clearness to refrain from constant reference to these or any discussion as to their value.

The proboscis consists of two parts, a proximal membranous conical portion—the rostrum and a distal half the proboscis proper which bears the oral lobes. The term haustellum is also used for this distal half (minus the oral lobes), and as a name it is probably more convenient, as the term proboscis is used for the whole structure—rostrum, haustellum, and oral lobes.

The rostrum (fig. 13, *Ros.*) is attached to the edges of the proboscis aperture, that is to the epistomium, genæ, and the gulo-mental plate. It has the shape of a truncated cone, and bears on the anterior side a pair of palps, which bear sensory setæ of two sizes.

The haustellum (fig. 13, *H.*), or proboscis proper, is attached to the distal end of the rostrum. The posterior side is formed by a convex, somewhat heart-shaped sclerite—the theca (figs. 1 and 3, *th.*) which probably represents a portion of the labium. The lower angle of the theca is incised by a semicircular sinus. By means of this the theca rests on a triradiate chitinous sclerite—the furca, which consists of a median, slightly convex rod (fig. 1, *f.*), from the

anterior end of which two arms diverge and form the chief skeletal structures of the oral lobes. The lower end of the theca rides on this structure, the bottom of the sinus resting on the median rod, and the two-pointed lateral terminations of the theca rest on the arms. In this manner these processes, in a state of repose, keep the arms of the furca closely approximated. The result of this will be seen later in studying the musculature of the proboscis.

The sides of the haustellum are membranous. On its anterior face, in a groove formed by the overlapping membranous sides, lie the labrum-epipharynx and labium-hypopharynx. The labrum-epipharynx (figs. 1 and 3, *lep.*) is attached at its proximal end to the membranous rostrum, but is incapable of a labral-like movement on account of its close connection with the labium-hypopharynx. Two slightly-curved, hammer-shaped apodemes (fig. 1, *ap.*) are attached to the proximal end of the labium-epipharynx. They assist in folding the proboscis during retraction, as will be shown later. The labium-epipharynx is shaped like a blunt arrow-head; the external surface is somewhat flattened. It is composed of two pairs of sclerites, an outer pair enclosing an inner pair, which form the pharyngeal channel. The edges of the inner tube are connected by a groove with the hypopharyngeal portion of the labium-hypopharynx, as shown in fig. 3. The labium-hypopharynx (fig. 3) represents the fusion of the hypopharynx with the greatly modified and fused second maxillæ or labium. It consists of a sclerite, curved in section, having the chitinous hypopharyngeal tube (fig. 3, *hp.*) fused to it along the upper half of its length. The edges of the hypopharyngeal tube engage with those of the inner pair of sclerites of the labium-epipharynx, as mentioned before. Distally the hypopharyngeal tube becomes free from the labium, as shown in fig. 3, and ends in a point where the lingual salivary duct opens.

Down each side of the labium-hypopharyngeal sclerite a rod-like thickening runs. Distally these thickened margins (paraphyses of Lowne) articulate with the discal sclerites.



The discal sclerites (fig. 1, *ds.*) are united at the posterior end to form, when the oral lobes are expanded, a U-shaped structure, with the limbs constricted in the middle where the ends of the thickened margins of the labium-hypopharynx articulate. They are sunk in deeply between the two oral lobes at the base of the oral pit with the free ends of the U anterior, these being spatulate and curved anteriorly.

The two oral lobes are normally connected by a bead and groove attachment along their anterior edges, but under pressure the connection is severed, and the oral disc presents a heart-shaped instead of the normal oval appearance. The oral lobes are covered on their upper aboral surfaces by sensory setæ, the large marginal setæ being different in structure from the rest. On the lower or oral surface a large number of channels, the pseudotracheæ (fig. 1, *ps.*) run from the internal margins of the oral lobes to the external borders. The channels of the pseudotracheæ are kept open when the lobes are extended by means of small incomplete chitinous rings, which give the channels a tracheal appearance, hence their name. Each of these incomplete rings has one end bifid, and as the bifid ends alternate the opening into the channel has a zigzag appearance. The number of pseudotracheæ on each lobe is generally thirty-six, and they are grouped in three sets. The anterior set of twelve all run into a single large pseudotracheal channel running along the anterior inner margin of the lobe, and a posterior set of twenty-one all run into a channel running along the posterior inner margin; between these two sets three pseudotracheæ run direct into the oral aperture. The oral aperture lies at the base of the small oral pit, which is a space kept open between the oral lobes by means of the discal sclerites. The pseudotracheæ do not extend as far as the discal sclerites, but on entering the oral pit the rings cease and the sides of the channels are covered by overlapping teeth, which extend back to the discal sclerites. Between the pseudotracheæ the membranous surface of each oral lobe is thrown into two longitudinal sinuous ridges, and projecting up from the

bottom of the furrows are several papillæ, generally four or five to each interpseudotracheal area, of a gustatory nature—the gustatory papillæ (figs. 1 and 18, *gp.*).

The Fulcrum.—This chitinous portion of the pharynx (fig. 1, *F.*) lies on the lower part of the head and in the rostrum. Kraepelin describes it as being shaped like a Spanish stirrup iron. Its structure will be best understood by referring to the figures. It consists of an outer portion, which is U-shaped in section; the basal portion, which is posterior and forms the floor of the pharynx (which Lowne, unfortunately, terms the hypopharynx) is vertical when the proboscis is extended. This basal portion is evenly rounded at both ends, and at the sides of the upper end there is a pair of processes—the posterior cornua (fig. 1, *pc.*) which serve for the attachment of muscles. The sides of the fulcrum are somewhat triangular in shape; their upper anterior portions are produced to form the anterior cornua (*a.c.*); here the sides bend inwards at right angles, and meet below the epistominum, upon which the fulcrum is hinged. The fulcrum is therefore quadrilateral in section at the upper proximal end, and trilateral at the lower distal end. The basal portion (fig. 2, *b.p.*) forms the floor of the pharynx; the roof of the pharynx is formed by another chitinous piece (*r.p.*) with a median thickened raphe. This roof lies parallel with the basal piece, and is fused with the sides of the fulcrum. On the membranous wall of the pharynx, between the labium-hypopharynx and the fulcrum, a small chitinous sclerite (fig. 1, *k.*) is developed, which Lowne terms the hyoid sclerite. It is U-shaped in section, and serves to keep the lumen of the pharynx in this region distended.

## 2. The Thorax.

As in all Diptera the possession of a single pair of wings has resulted in the great development of the mesothorax at the expense of the other thoracic segments, consequently the thorax is chiefly made up of the sclerites composing the

mesothorax. The prothorax and metathorax compose very small portions on the anterior and posterior faces respectively. Seen from above the thorax is oviform with the blunt end anterior and slightly flattened. Three transverse sutures on the dorsal side mark the limits of the prescutum, scutum, and scutellum of the mesothoracic segment; the mesothoracic scutellum forms the pointed posterior end, and slightly overhangs the anterior end of the abdomen.

The Prothorax.—The prothoracic segment has been reduced to such an extent that it is hopeless to attempt to homologise all the separate sclerites with those of a typical thoracic segment. To obtain a complete view of the prothorax it is necessary to examine it from the anterior end after the removal of the head. The following sclerites can then be recognised. The prosternum is a median ventral plate, quadrilateral in shape having the anterior end rounded and broader than the posterior end. It does not occupy the whole of the prosternal area, but is bounded by the prosternal membrane. Internally a ridge runs to the posterior end of the prosternum and bifurcates, each ridge running to the posterior corners, to which two strong processes (the hypotremata of Lowne) are attached. In front of the prosternum there is a small saddle-shaped sclerite which, on account of its position, may be called the interclavicle (the sella of Lowne). Two lobes at its anterior end are covered with small processes, probably sensory in function. A pair of small sclerites is situated in front of these lobes; these sclerites with the interclavicle no doubt belong to the prosternum. The interclavicle is ventral to the cephalothoracic foramen. The jugulares (3me jugulaires of Kunckel d'Herculais) are two prominent pocket-shaped sclerites lying one on each side of the cephalothoracic foramen, and having their convex faces external. Lying immediately below each of the jugulares is a small rod-like sclerite—the clavicle. The dorsal region of the prothorax the pronotum (fig. 6 *pr.n.*) is formed by two sclerites united in the median line, their dorsal sides being curved. From the ventral side of the pronotum a pair of

chitinous apodemes project into the thoracic cavity. The lateral regions of the pronotum are in contact with the humeri and the prothoracic episterna. The humeri (*hu.*) are a pair of strongly convex sclerites situated in the anterolateral region of the thorax. They are bounded above by the presentum of the mesothorax, internally and below by the episterna of the prothorax, and externally by the lateral plate of the mesosternum and the anterior thoracic spiracle. Its inner concave surface serves for the attachment of the muscle of the prothoracic coxa. The episterna (*eps.*) (epitrochlear sclerites of Lowne) are comparatively large sclerites forming the lateral regions of the prothorax. They overhang the attachments of the prothoracic limbs. The internal skeleton of the prothorax consists of the two stout hollow apodemes—the hypotremata mentioned previously. They arise from the postero-lateral edges of the prosternum, and run obliquely across the ventral edge of the anterior thoracic spiracle where the hypotreme divides, the posterior branch runs up the posterior margin of the spiracle, between the lateral plate of the mesosternum and the peritreme (the chitinous ring surrounding the spiracle), the anterior branch fuses with the prothoracic episternum.

The Mesothorax.—The notum of the mesothorax occupies the whole of the dorsal side of the thorax. It is composed of the four sclerites to which Audouin (1824) gave the name of prescutum, scutum, scutellum, and postscutellum. The prescutum (*prs.*) forms the anterior part of the dorsal region of the thorax. Its anterior portion bends down almost vertically to unite with the pronotum. The anterior edge of the prescutum is inflected after the pronotal suture, and is produced in the median line into a small bifurcating process. The prescutum is bounded laterally by the humerus and a membranous strip—the dorso-pleural membrane. The scutum (*se.*) is the largest of the mesonotal plates. It occupies the whole of the median dorsal region of the thorax. Anteriorly it is bounded by the prescutum, laterally by the alar membrane and the lateral plate of the postscutellum, and posteriorly by

the scutellum. From the lateral region of the scutum a process projects forwards and downwards, and articulates with the posterior portion of the wing-base (the metapterygium). The scutellum (*sctl.*) is a triangular pocket-shaped sclerite which overhangs the postscutellum and the base of the abdomen. The posterior surface of the thorax is chiefly composed of the large postscutellum. This is made up of three pieces, a median escutcheon-shaped plate (*mpsc.*) strongly convex to the exterior, and two convex lateral plates (*lp.sc.*). The lateral plates are bounded below by the metasternum and spiracles, and anteriorly by the pleural region of the mesothorax.

The mesosternum is a sclerite of considerable size and forms the keel of the thorax. It consists of a median ventral portion (*ms.*) which is produced laterally to form two large lateral plates (*lp.*). The median portion is bounded in front by the prosternum and the foramina of the anterior coxæ, and behind by the median coxal foramina. A short distance behind the anterior end a depression in the mid-ventral line extending to the posterior edge indicates a median inflection forming the entothorax. The lateral regions of the posterior margins of the mesosternum are inflected on each side to form the entopleura. The lateral plates of the mesosternum form the whole of the anterior portion of the pleural region; each is bounded in front by the humerus, spiracle, and prothoracic episternum, and above by the dorso-pleural membrane, and behind by the mesopleural membrane. The ventral side of the lateral plate is continuous in front with the median plate of the mesosternum, and behind is united by means of a suture. The remaining portion of the mesopleural region is made up of the episternum, epimeron, and two small sclerites connected with the wing-base—the parapteron and costa. The episternum (*eps.*) is situated behind the mesopleural membrane and below the alar membrane, below and behind it is bounded by the epimeron. Its surface is marked by two convexities, the ampullæ, the upper of the two corresponding to Lowne's great ampulla of the blowfly. The dorsal side of



the episternum is intimately connected with the sclerites<sup>1</sup> of the anterior portion of the wing-base.

The epimeron (*ep.*) is a triangular sclerite, and is bounded below by the mesosternum and metasternum, behind by the lateral plate of the postscutellum, and above by the episternum and alar membrane. The parapteron (*pt.*) is a sclerite situated at the top of the mesopleural membrane. The greater portion of it is internal, only a small triangular portion can be seen externally. Internally this is continued as a cruriform sclerite to which are attached important muscles controlling the wings. The costa (*ca.*) is a small sclerite situated on the dorsal margin of the epimeron. The internal skeleton of the mesothorax consists of the entothorax, entopleura, mesophragma, and the inflected edges of the episterna and epimera. The entothorax is composed of a median vertical plate subtriangular in shape, on the top of which a median plate produced laterally into wing-like processes rests. On this structure the thoracic nerve-centre lies. The entopleura and the inflected edges of the episterna and epimera all serve for the attachment of wing muscles. The mesophragma (*mph.*) is a convex sclerite fused with the lower edge of the postscutellum. Its posterior edge is incised in the middle and forms the dorsal arch of the thoraco-abdominal foramen.

The Metathorax.—The largest sclerite of the greatly reduced metathorax is the metasternum (*mts.*). It is a wing-shaped sclerite with the narrow transverse portion situated between the coxal foramina of the median and posterior pairs of legs; the expanded lateral portions form the wall of the thorax above the insertions of these legs. The edges of the narrow transverse strip are inflected, and unite the lateral portions of the metasternum. A trough-shaped longitudinal fold—the metafurca rests on the narrow transverse portion of

<sup>1</sup> In this account the individual sclerites which compose the wing base will not be described. Lowne has described them at great length for the blowfly, and although the wing-base sclerites of *M. domestica* differ slightly in shape from those of *Calliphora*, Lowne's description of their relations holds good for the former insect.

the metasternum. The posterior end of the metafurca bends downwards and articulates with the posterior coxæ on each side. The metafurca serves for the attachment of the thoraco-abdominal muscles. The pleural region of the metathorax is a narrow triangular space situated behind the lateral portion of the metasternum and the posterior coxæ. It is composed of a narrow triangular episternum and epimeron. The former (*eps.*''') is bounded in front by the metasternum, the posterior thoracic spiracle and the base of the haltere, below by the posterior coxal foramen, and behind by the epimeron. The epimeron (*ep.*'') is also bounded below by the coxal foramen and behind by the narrow dorsal arch of the metathorax and the first abdominal segment, its apex comes in contact with the base of the haltere. The dorsal region of the metathorax has practically disappeared, all that can be recognised as metanotum is a narrow chitinous strip (*mn.*) on each side between the apex of the metapleural area and the dorsal edge of the first abdominal area.

Wings.—The wings are situated at the sides of the scutum on the alar membrane, to which are attached the sclerites of the wing base. They are covered with very fine hairs.

In describing the neurature of the wings the nomenclature proposed by Comstock and Needham (1898) for the wings of the whole group of insects will be employed.

The nervures of the wing are ocreaceous. The anterior edge of the wing (fig. 16) is formed by a stout nervure, the costa ( $C_1$ ), which is very setose. The second longitudinal nervure, the subcostal ( $Sc_1$ ), joins the costal about half way along its length. A small transverse nervure, the humeral ( $h$ ), divides the costal cell into costal ( $C$ ) and first costal ( $1C$ ) cells. The next main nervure—the radial—divides into a number of branches (in the typical insect five); some of these have coalesced in the fly. A nervure joining the costal just past the middle is the first radial ( $R_1$ ) cutting off the subcostal cell. The next nervure, which joins the costal on the apical curve, represents the fused second and third radial nervures

(*R.* 2 + 3). This cuts off the first radial cell (1 *R.*). The last nervure, which joins the costal almost at the apex of the wing, represents the fused fourth and fifth radial nervures (*R.* 4 + 5), and so cuts off the third radial cell (3 *R.*). The fourth main longitudinal nervure is the median, which, in the typical insect, divides into three, but in the fly the nervures have undergone coalescence, as will be shown. The first and second median nervures have coalesced (*M.* 1 + 2), and do not run direct to the margin of the wing, but bend forwards and almost meet *R.* 4 + 5 on the costa. About half way across the wing a transverse nervure, the radio-medial (*rm.*) unites *R.* 4 + 5 and *M.* 1 + 2, and cuts off the fifth radial cell (5 *R.*) from the radial (*R.*). The next longitudinal nervure represents the coalesced third medial and cubital nervures (*M.* 3 + *Cu.* 1). It runs to the posterior margin of the wing about half way along the length of the latter. The nervures *M.* 1 + 2 and *M.* 3 + *Cu.* 1 are united by two transverse nervures. The proximal nervure—the medio-cubital (*m.cu.*) cuts off the small triangular medial cell (*M.*); the distal transverse nervure (*m.*) cuts off the first second medial cell (2 *M.*<sup>1</sup>) from the second second medial cell (2 *M.*<sup>2</sup>). The last longitudinal nervure—the anal (*A.*<sub>1</sub>)—is undivided, and does not reach the margin of the wing, thus incompletely separating the first cubital (1 *Cu.*) and anal (*A.*) cells. A small transverse nervure, the cubito-anal (*cu.a.*), slightly more proximal than the medio-cubital, cuts off the small triangular cubital cell (*Cu.*) from the first cubital cell (1 *Cu.*). Running parallel with, and posterior to, the anal longitudinal nervure, there is apparently another nervure. This, however, is not a true nervure, but is merely a chitinised furrow giving additional strength to the posterior angle of the wing. The posterior edge of the base of the wing is divided into a number of lobes. These are the anal lobe, and, as Sharp (1895) proposed, the alula, antisquama, and squama. The squama is thicker than the rest, and is attached posteriorly to the wing root between the mesoscutum and the lateral plates of the



postscentellum. It covers the haltere, as in all "calyptrate" Muscidae.<sup>1</sup>

The Halteres.—The halteres or balances (fig. 6, *hal.*) are generally considered to represent the rudimentary metathoracic wings. They are covered by the squamæ, and are situated on the sides of the thorax above the posterior thoracic spiracles. Each consists of a conical base on which are a number of chordonotal sense-organs, and on this base is mounted a slender rod, at the end of which a small spherical knob is attached. The wall of the distal half of this sphere is thinner than the proximal half, and in preserved specimens is generally indented. Experiments show that the

<sup>1</sup> The nomenclature of Comstock and Needham has not yet been adopted by dipterologists in general; but, on account of its great morphological value, it will no doubt in course of time replace the present confused system. It may therefore be useful if the nomenclature employed in the foregoing description be compared with those most usually employed.

Longitudinal nervures.—*C*<sub>1</sub>. Costal. *Sc*<sub>1</sub>. Mediastinal, auxiliary. *R*<sub>1</sub>. Subcostal, 1st longitudinal. *R*. 2 + 3. Radial, 2nd longitudinal. *R*. 4 + 5. Cubital, 3rd longitudinal; ulnar (Lowne). *M*. 1 + 2. Median, 4th longitudinal; discal (Verrall). *M*. 3 + *Cu*<sub>1</sub>. Submedian, 5th longitudinal; postical (Verrall). *A*<sub>1</sub>. Aual, 6th longitudinal. Pseudonervure, axillary, 7th longitudinal.

Transverse nervures.—*h*. Humeral, 1st transverse; basal cross vein (Verrall). *rm*. Discal, 2nd transverse; middle cross vein (Verrall); medial transverse; anterior transverse (Austen). *m-cu*. Anterior basal transverse (Austen); lower cross vein (Verrall); postical transverse (Lowne). *m*. Posterior transverse (Austen); postical cross vein (Verrall); discal transverse (Lowne). *cu-a*. Posterior basal transverse (Austen); anal cross vein (Verrall); anal transverse (Lowne).

Cells.—*C*. Costal. 1 *C*. Second costal. *Sc*. Third costal (Lowne correctly calls this "sub-costal"). 1 *R*. Marginal. 3 *R*. Sub-marginal; cubital (Lowne). 5 *R*. First posterior cell (Austen); sub-apical (Lowne and Verrall). 2 *M*<sup>2</sup>. Second posterior cell (Austen); apical. 1 *Cu*. Third posterior cell (Austen and Verrall); patagial (Lowne). 2 *M*<sup>1</sup>. Discal (this term is used also in Lepidoptera, Trichoptera, and Psocoptera, and in each family refers to a different cell!). *R*. Anterior basal cell (Austen); upper or 1st basal or radical (Verrall); prepatagial (Lowne). *M*. Posterior basal cell (Austen); middle or 2nd basal or radical (Verrall); anterior basal (Lowne). *Cu*. Aual cell (Austen); lower or 3rd basal or radical (Verrall); posterior basal (Lowne).

halteres are organs of a static function. They are not balancing organs in the sense that they are equivalent to the balancing pole of a rope-walker. They also have probably an auditory function. They are innervated by the largest pair of nerves in the thorax.

The Legs.—The three pairs of legs are composed of the typical number of segments. Each consists of coxa, trochanter, femur, tibia, and tarsus. The coxæ are the only segments which show any considerable difference in the three pairs of legs. The anterior coxæ are comparatively large and boat shaped, the intermediate coxæ are smaller and their separate sclerites more marked; the coxal plates of the intermediate coxæ are shown in fig. 6 (*cp.*). The coxal joints of the posterior pair of legs are almost similar to those of the intermediate pair. The anterior femora are shorter and stouter in the middle than those of the intermediate posterior pairs of legs. The anterior tibiæ are also shorter than those of the succeeding legs. The anterior tibiæ are covered on their inner sides with closely-set, orange-coloured setæ which serve as a comb by means of which the fly removes particles of dirt adhering to the setæ which clothe its body; the first tarsal joints of the posterior legs are also similarly provided. The tarsi consist of five joints, the terminal joints bearing the "feet." These organs about which so much has been written consist of a pair of curved lateral claws or "ungues" which subtend a pair of membranous pyriform pads—the pulvilli. The pulvilli are covered on their ventral sides with innumerable, closely-set, secreting hairs by means of which the fly is able to walk in any position on highly polished surfaces. A small sclerite lies between the bases of the pulvilli. The tarsal joints and the other segments of the legs are covered with a large number of setæ.

### 3. The Abdomen.

The abdomen is oviform with the broad end basal. The total number of segments which compose the abdomen is eight in the male and nine in the female. The visible portion con-

sists of apparently four segments in the male and female, in reality there are five as the first segment has become very much reduced, and has fused with the second abdominal segment forming the anterior face of the base of the abdomen (see fig. 8). The segments succeeding the fifth are greatly reduced in the male, and in the female they form the tubular ovipositor which, in repose, is telescoped within the abdomen. The second, third, fourth, and fifth abdominal segments are well developed, and consist of a large tergal plate, which extends laterally to the ventral side. The sternal plates are much reduced, and form a series of narrow plates lying on the ventral membrane along the mid-ventral line. The spiracles are situated on the lateral margins of the tergal plates. The sclerites of the abdomen which are exposed are strongly setose, especially the fourth and fifth dorsal plates, but they do not bear macrochæbæ.

#### IV. INTERNAL STRUCTURE.

##### 1. The Muscular System.

The muscular system of the fly is similar to that of *Volucella*, described by Kunckel d'Herculais (1881), and of the Blow-fly, described by Lowne and Hammond, and consequently they will be but briefly described. The muscles may be divided into the following groups: 1. Cephalic, 2. Thoracic, 3. Segmental, 4. Those controlling the thoracic appendages, and 5. Special muscles.

1. The cephalic muscles will be considered in the detailed description of the head.

2. The thoracic muscles are enormously developed and almost fill the thoracic cavity. They are arranged in two series. The dorsales (figs. 13 and 15, *do.*) are six pairs of muscle-bands on each side the median line, attached posteriorly to the postscutellum and mesophragma, and anteriorly to the prescutum and anterior region of the scutum. The sternodorsales (*st.do.*) are vertical and external to the dorsales and are arranged in three bundles on each side. The first

two pairs have their upper ends attached to the presentum and scutum, and their lower ends inserted on the mesosternum, the third pair is attached dorsally to the scutum and ventrally to the lateral plate of the postscutellum above the spiracle. As Hammond has shown in the blowfly (1881) all these muscles are mesothoracic. The dorsales by contraction loosen the alar membrane and so depress the wing, the sternodorsales have the opposite effect.

3. The segmental muscles. These muscles, which are so prominent in the larva, have almost disappeared in the imago. They are represented by the cervical muscles, certain small thoracic muscles, the thoraco-abdominal muscles, and the segmentally-arranged abdominal muscles together with the muscles controlling the ovipositor and male gonapophyses.

4. The muscles controlling the thoracic appendages, the wings, legs, and halteres. There is an elaborate series of muscles controlling the roots of the wing, but in order to avoid too much detail they will not be described here. The flexor muscles of the anterior coxæ have their origin on the inner surfaces of the humeri, a fact supporting the prothoracic nature of these sclerites; the flexors of the middle pair of legs have their origin on the sides of the posterior region of the prescutum. The internal muscles of the leg are similar to those of the blowfly and *Volucella*.

5. Special muscles. These are the muscles controlling the spiracular valves, the penis, and other small muscles.

## 2. The Nervous System.

The central nervous system (fig. 11) consists of (1) the brain or supracæsophageal ganglia which are closely united with the subcæsophageal ganglia, the whole forming a compact mass which I propose to call the cephalic ganglion (fig. 1, *C.G.*), perforated by a small foramen for the passage of the narrow cæsophagus, and (2) the thoracic compound ganglion which is composed of the fused thoracic ganglia with the abdominal ganglia. The two compound nerve-centres are

united by a single median ventral cord running from the subœsophageal ganglia to the anterior end of the thoracic nerve-centre.

The cephalic ganglion consists of the supracœsophageal ganglion and the subœsophageal ganglia so closely united that the commissural character of the circumœsophageal connectives is quite lost. Externally, on the dorsal side of the brain three longitudinal fissures can be seen, a median fissure and two lateral fissures marking the origin of the optic lobes.

The supracœsophageal ganglia. The characters of the ganglia composing the brain are hidden by the sheath of cortical cells which fills up the spaces between the ganglia, the characters of these can be ascertained by the serial sections. The median mass the procerebrum is formed by the fusion of the procerebral lobes. These are united before and behind, and enclose a central ganglionic mass—the central body. Behind the procerebrum two pairs of fungiform bodies arise. On the anterior face of the procerebrum the antennal or olfactory lobes which represent the deutocerebrum are situated laterally. Each sends a nerve (figs. 1 and 11, *an.n.*) to the antenna. Above these and on the dorsal side are a pair of lobes—the frontal lobes contiguous with each other in the median line—these belong morphologically to the tritocerebrum. Posterior to these in the median dorsal line of the cerebrum a single median nerve, the ocellar nerve (figs. 1 and 11, *oc.n.*), arises; this runs vertically to the ocelli. A pair of lobes which correspond to Lowne's thalami of the blowfly are situated external to and between the frontal and antennal lobes. The peduncles of the optic lobes have their origins from the sides of the procerebrum. Each optic peduncle (fig. 11, *O.P.*) contains three ganglionic masses which Hickson (1885) has termed from the brain peripherally the opticon, epipticon, and periopticon (fig. 1, *P.O.*) respectively.

The subœsophageal ganglia (fig. 1, *S.O.*). The commissures uniting the supracœsophageal ganglia to the œsophageal mass cannot be recognised as such, owing to the extreme state of cephalisation of the cephalic ganglia. They are



represented by the regions lateral to the œsophageal foramen, and from the anterior side of each of them arises a pharyngeal nerve (figs. 1 and 11, *ph.n.*). From the ventral side of the subœsophageal ganglia a pair of nerves—the labial nerves (fig. 1, *lb.n.*)—arise and run down the proboscis, innervating the muscles of that organ; on reaching the oral lobes they bifurcate and branch freely, supplying the numerous sense organs in those structures. The cortical cells (Leydig's "Punksubstanz"), which fill up the spaces between the ganglia and form an investing sheath round the whole ganglionic mass, are of two kinds. The smaller cells are rounded, their nuclei are large in proportion to the protoplasm, and their protoplasmic fibres anastomose with each other. Among these smaller cortical cells, and also occasionally in the ganglionic substance, larger ganglionic cells occur, their protoplasm taking the stain very readily. Unipolar, bipolar, and tripolar ganglion cells are found.

The eyes. Each eye contains about 4000 facets. They are similar in all respects to the eyes of the blowfly, which have been fully described by Hickson (*loc. cit.*), whose results my study confirms; consequently, a description of their structure will not be given. It should be noted that, in spite of the fact that Hickson corrected many mistaken views held by Lowne in his memoir (1884), these are repeated in his monograph of the Blowfly.

The cephalo-thoracic nerve cord (fig. 11, *c.n.*) unites the cephalic and thoracic ganglia. Near its junction with the thoracic ganglion a pair of cervical nerves (*cer.n.*) arise, innervating the muscles of the neck.

The thoracic ganglion (figs. 12 and 14) is pyriform, with the broad end anterior, and rests on the entothoracic skeleton of the mesothorax. As in the cephalic ganglion, the component ganglia are ensheathed in a cortical layer, which is of the same nature. The nerves of the three pairs of legs (*pr.cr.*, *ms.cr.*, *mt.cr.*) arise from three large ganglia, which are the prothoracic (*Pr.G.*), mesothoracic (*Ms.G.*), and meta-thoracic (*Mt.G.*) ganglia. These are united by a median

longitudinal band of nerve tissue, which runs dorsal to them, and behind the metathoracic ganglia swells out into a ganglionic mass (*A.G.*), which represents the abdominal ganglia. In this median dorsal band there is a median dorsal fissure stretching posteriorly from above the middle of the mesothoracic ganglia. The dorsal regions of the mesothoracic and metathoracic ganglia show ganglionic swellings. From the antero-dorsal sides of the prothoracic ganglia a pair of prothoracic dorsal nerves (*pr.d.*) arise and supply the muscles of that region, including those of the anterior thoracic spiracle. The nerves supplying the mesothoracic legs (*ms.cr.*) arise from the postero-ventral sides of the mesothoracic ganglia. Between the mesothoracic ganglia there is a median ganglionic mass, situated slightly dorsal, from the middle region of which the nerve-fibres of the large pair of dorsal mesothoracic nerves (*m.s.d.*) arise; Lowne, in the blowfly, calls these prothoracic. The roots of these nerves are broad dorsoventrally. These nerves innervate the sterno-dorsales muscles of the middle region. In this median mesothoracic nerve centre, posterior to the origin of the dorsal mesothoracic nerves, the fibres of a pair of nerves, the accessory dorsal mesothoracic nerves (*ac.ms.*), have their origin; these appear externally to arise dorsal to the roots of the mesothoracic crural nerves. The dorsal metathoracic nerves (*mt.d.*), which innervate the halteres, and are the largest pair of thoracic nerves, have their origin from the median dorsal band in front of the metathoracic ganglia, so that they appear to be almost mesothoracic in origin. The metathoracic crural nerves (*mt.cr.*) arise from the posterior-ventral sides of the metathoracic ganglia. Posterior to these a pair of slender nerves, the accessory dorsal metathoracic nerves, have their origin, and innervate the muscles at the posterior end of the thorax.

The dorsal band becomes much thinner posterior to the abdominal ganglion, and runs into the abdomen as a median abdominal nerve (*ab.n.*). In the thorax two pairs of abdominal nerves arise. In the abdomen the abdominal nerves

arise alternately and irregularly from the median abdominal nerve. The median abdominal nerve finally terminates in the genitalia.

### 3. The Alimentary System.

The alimentary canal of the house-fly is shorter than that of the blowfly, and also than that of *Glossina* described by Minchin (1905), and slightly longer than the alimentary tract of *Stomoxys* described by Tulloch (1906). It serves as a good example of the Muscid digestive canal. It is of a suctorial character, and consists of pharynx, œsophagus, crop, proventriculus, ventriculus or chyle stomach, proximal and distal intestine and rectum.

The pharynx has already been described, and will be further referred to in the detailed description of the head. At the proximal end of the fulcrum, where the œsophagus arises, there is usually a small mass of cells, which Kraepelin has described as glandular, but which I believe to be simply fat-cells.

The œsophagus (figs. 1, 17, 20, *œs.*) commences at the proximal end of the pharynx, and describes a curve before passing through the œsophageal foramen in the cephalic ganglion, where it narrows slightly. It then passes through the cervical region into the thorax in the anterior region, of which it opens into the proventriculus (figs. 17, 20, *Pr.*), continuous with, and in the same line as the œsophagus, the duct leading to the crop (fig. 20, *d.cr.*) passes along the thorax dorsal to the thoracic nerve-centre, and entering the abdomen it leads into the crop, which lies on the ventral side of the abdomen. The œsophagus has a muscular wall, enclosing a layer of flat epithelial cells, and is lined by a cuticular intima, which is thrown into several folds at the anterior end.

The crop (fig. 17, *Cr.*) is a large bilobed sac, capable of considerable distension, and, when filled with the liquid food, it loses its bilobed shape, and occupies a large portion of the



antero-ventral region of the abdomen. Its walls exhibit muscular (unstriated) fibres; the flat epithelial cells have a very thin cuticle.

The proventriculus (*Pv.*) is circular and flattened dorso-ventrally. Its structure will be understood by reference to fig. 20. In the middle of the ventral side it opens into the œsophagus, and on the dorsal side the outer wall is continued as the wall of the ventriculus (*Ven.*). The interior is almost filled up by a thick circular plug (*Pv.p.*), the cells of which have a fibrillar structure, and it is pierced through the centre by the œsophagus. The neck of the plug is surrounded by a ring of elongate cells, external to which the wall of the proventriculus begins, and, enclosing the plug at the sides and above, it merges into the wall of the ventriculus. I do not agree with Lowne in regarding the proventriculus as "a gizzard and nothing more," but its structure suggests a pumping function and also that of a valve. On the dorsal side of the œsophagus, at its junction with the proventriculus, a small ganglion, the proventricular ganglion (*Pv.g.*), lies, communicating by a fine nerve with the cephalic ganglion.

The ventriculus, or chyle stomach (figs. 17, 20, *Ven.*), represents the anterior region of the mesenteron, the posterior region of the latter being formed by the proximal intestine. It is narrow in front, and widest in the posterior region of the thorax, where it again narrows in passing through the thoraco-abdominal foramen into the abdomen to become the proximal intestine. Except in the anterior and posterior regions, where columnar cells compose the digestive epithelium, the walls of the ventriculus are thrown into a number of transverse folds, which are again subdivided longitudinally, the result being the formation of small crypts or sacculi, which are lined by large cells. These sacculi correspond to the digestive cœca of other insects.

The proximal intestine (figs. 17, 21, *p.int.*) is the longest region of the gut. It varies in length considerably. In the normal-sized condition its course is as follows:—Beginning at the anterior end of the abdomen it runs dor-

sally beneath the heart to the posterior region, where it curves downwards, turns to the left, and runs forward for a short distance, curving to the right, where it doubles back transversely to the left. Here it doubles sharply back to the right, from whence it runs forward for a little way, and crosses over to the left. Curving, it runs posteriorly to become the distal intestine. Its walls are lined by an epithelium of large columnar cells.

The distal intestine (*d.int.*). The junction of this with the proximal intestine is marked by the entrance of the ducts of the malphigian tubes. It runs posteriorly, and curves dorsally and forwards to become the rectum, from which it is separated by a cone-shaped valve—the rectal valve, the position of which is marked externally (fig. 21, X.). The epithelium of the distal intestine consists of small cubical cells, which project into the lumen, and are covered by a fairly thick chitinous intima. The epithelial wall of the distal intestine is thrown into usually about six longitudinal folds.

The rectum (*rect.*) is composed of three parts, an anterior region, an intermediate region which is swollen to form the rectal cavity, and a shorter region posterior to this which opens externally by the anus. The anterior region is lined by cubical cells, whose internal faces project into the lumen of the rectum, and give the chitinous intima a tuberculated structure. The intermediate region which forms the rectal cavity contains the four rectal glands (*rect.gl.*). Its walls are lined by a thin cuticle supported by a flattened epithelium. The posterior portion of the rectum is short, and has thick muscular walls. The cuticular intima is continuous with that of the external skeleton.

Salivary Glands.—There are two sets of salivary glands—a pair of labial and a pair of lingual glands. The structure of the labial glands will be described in the account of the anatomy of the head.

The lingual glands (fig. 17, *sl.g.*), though considerably longer than the total length of the body, are of the simplest

tubular type. They are of uniform width throughout their whole length, except the slightly swollen blind termination. These blind ends lie one on each side of the ventral and posterior region of the abdomen, generally embedded in the fat-body. They take a sinuous course forwards through the abdomen into the thorax, where they run alongside the ventriculus. At the sides of the proventriculus they are thrown into several folds, which appear to be quite constant in character. They pass forwards at the sides of the œsophagus and on entering the cervical region the ducts lose their glandular character, and assume a spiral thickening; before leaving the cervical region the two ducts unite below the œsophagus, and the single median duct enters the head ventral to the cephalothoracic nerve cord, and runs direct to the proximal end of the hypopharynx, at the end of which it opens. A short distance before entering the hypopharynx the salivary duct (fig. 1, *sal.d.*) is provided with a small valve controlled by a pair of fine muscles (*s.m.*), which serves to regulate the flow of the salivary secretion. The glands are composed of glandular cells (fig. 22), which are convex externally, and have a fibrillar appearance in section. No vacuoles have been found in the cells.

**The Malpighian Tubes.**—A pair of malpighian tubes (fig. 21, *malp.*) arises at the point of junction of the proximal and distal intestines, that is, where the mesenteron joins the proctodæum. Each malpighian tube shortly divides at an angle of  $180^{\circ}$  into two malpighian tubules. The malpighian tubules are very long and convoluted, and intimately bound up with the diffuse fat-body, so that it is a matter of considerable difficulty to dissect them out entire. They have a moniliform appearance and are of uniform width throughout; never more than two cells can be seen in section. They are generally yellowish in colour. As in most insects they are undoubtedly of an excretory nature, as the contents of the cells and tubules show. Lowne's view that, in the blowfly, they are of the nature of a hepato-pancreas is untenable morphologically and physiologically.

The Rectal Glands.—The four rectal glands (*rect.gl.*) are arranged in two pairs, two on each side of the rectal cavity. Each rectal gland (fig. 25) has a conical or pyriform apex with a swollen circular base. It is composed of a single layer of large columnar cells (*r.gl.*), the papilla being hollow, with the cavity in communication with the general body cavity. It is covered externally by a perforate chitinous sheath (*sh.*), which is continuous with the intima of the rectum. A number of tracheæ (*tr.*) enter the cavity of each gland, and fine tracheæ may be seen penetrating the wall. The cavity of the gland is filled with a loose tissue of branching cells. As the gland is capable of pulsation there is no doubt a constant interchange of blood between the cavity of the gland and the body cavity (which is a hæmocœl). By this means waste products may be extracted from the blood by the large gland cells and excreted into the rectum through the pores on the external sheath of the gland. The rich supply of tracheæ probably assists the cells in the process of excretion, as we find the tracheæ very numerous, and intimately connected with the malpighian tubules.

#### 4. The Respiratory System.

The respiratory or tracheal system is developed to a very great extent in the fly and occupies more space than any other anatomical structure. Only by dissection of the freshly-killed insect can one obtain a true conception of its importance. It consists of tracheal sacs of varying size having extremely thin walls and tracheæ which may arise from the sacs, or, in the case of the abdominal tracheæ, independently from the spiracles.

The Anterior Thoracic Spiracles (figs. 6 and 13, *a.th.*).—Each is a large vertical opening behind the humeral sclerite and above the anterior legs. It is surrounded by a chitinous ring, the peritreme and the opening is guarded by a number of dendritic processes which prevent the entrance of dust and other foreign bodies. It leads into a shallow chamber or

vestibule which communicates with the rest of the spiracular system through a valvular aperture.

The anterior thoracic spiracles supply the whole of the head, the anterior and median regions of the thorax, the three pairs of legs, and by means of the abdominal air-sacs a large part of the viscera.

Internal to the valve the tracheal system divides. The tracheal sacs springing from the posterior side are as follows : Ventrally a rather narrow tracheal duct leads into a sac—the anterior ventral thoracic sac (fig. 13, *a.v.s.*) situated at the side of the thoracic ganglion which it supplies. Above the origin of this another tracheal duct leads to a vertical sac supplying the anterior sterno-dorsales muscles. Dorsally the ducts of two sacs take their origin ; the smaller and more dorsal is a flat sac closely apposed to the anterior ends of the dorsales muscles (*do.*) which it supplies ; the more ventral of the two is one of the two most important branches of the anterior thoracic spiracle (the other being the branch supplying the head). In the thorax it takes the form of an elongated sac lying below the dorsales muscles, and by side of the alimentary canal. From the dorsal side of this the longitudinal thoracic sac (*l.tr.s.*) a number of branches arise which supply the lower dorsales muscles. It is constricted about the middle of its length and anterior to the constriction ; a branch is given off which supplies the ventral portion of the median sterno-dorsales muscles. In the posterior region of the thorax another ventral branch is given off from which branches arise, one supplying the ventral portions of the posterior sterno-dorsales muscles, the other opening into the posterior ventral thoracic sac (*p.v.s.*), which supplies the intermediate and posterior legs. The longitudinal thoracic sac then narrows, and passes through the thoraco-abdominal opening into the abdomen. In the abdomen it immediately dilates to form one of the large abdominal air-sacs (*a.b.s.*). The pair of abdominal air sacs in some cases occupy about half the total space of the abdomen. When the fat-body is not greatly developed they occupy almost the whole of the



basal portion of the abdomen. They give off internally a large number of tracheæ which ramify among the viscera and provide a large portion of the contents of the abdomen with air.

From the anterior side of the anterior thoracic spiracle a flattened sac arises. On its ventral side this gives off a branch which supplies the muscles of the neck and the anterior leg. The sac then narrows into a rather thick-walled cervical tracheal duct (*c.tr.*), which passes through the neck alongside the cephalo-thoracic nerve-cord and enters the head.

Tracheal Sacs of the Head.—The tracheal sacs of the head occupy the greater portion of the head capsule. They entirely fill up all the space which would otherwise be hæmo-cœl. These tracheal sacs are supplied by the cervical tracheal ducts which, on entering the head capsule, curve dorsally behind the cephalic ganglion. Before curving upwards each gives off a large ventral duct (fig. 4), which spreads out beneath the cephalic ganglion forming a structure of a tentorial nature upon which the ganglion rests. The dorsal cephalic ducts unite behind the cephalic ganglion above the œsophagus. From the point of junction three ducts arise, two lateral ducts and a median dorsal duct. The median dorsal duct (*m.d.*) opens into a large bilobed dorso-cephalic sac lying on top of the ganglion, and occupying the dorsal region of the head capsule. It gives off branching tracheal twigs supplying the antero-dorsal portion of the optic ganglion (periopticon). Each of the lateral ducts (fig. 4, *l.d.*) supplies the posterior cephalic sacs. It first communicates with a sac (fig. 13, *p.c.s.*) lying behind the dorsal portion of the optic ganglion to which it gives off a large number of tracheal twigs. This sac opens into an elongate vertical sac which occupies the ventro-posterior region of the head capsule. The remaining tracheal sacs of the head are supplied by the tentorial tracheal ducts (*tr.d.*), which spread out beneath the cerebrum in a fan-shaped manner, and are bilaterally distributed. Each half, in addition to giving off internally tracheal twigs to the optic

ganglia, communicates with two tracheal sacs. An internal duct leads into a large spherical sac, the anterior cephalic sac (*a.c.s.*) situated in the anterior region of the head dorsal to the fulcrum. From the dorsal side of this sac a branch is given off which supplies the antenna of its side; the ventral side is continued down the fulcrum as a narrow tracheal sac. The lateral portion of the tentorial tracheal duct opens into the ventro-lateral cephalic sac (*v.c.s.*) situated posterior to the optic ganglion. The lower end of this sac gradually narrows as it enters the rostrum which it traverses, giving off half-way along its length a trachea which supplies the palp of that side. On reaching the haustellum it takes the form of a trachea proper, having annular thickenings. Shortly after entering the haustellum it gives off two branches to the muscles of this region. The main trachea is continued into the oral lobe of its side where it divides into anterior and posterior branches, and these again divide into numerous small tracheæ running to the edges of the oral lobes. Lowne, in his description of the tracheal system of the blowfly, describes and figures the tracheal supply of the proboscis as being of the nature of tracheal sacs and capable of distension; he also describes a trefoil-shaped tracheal sac at the base of the oral lobes giving off very regular branches, the dilation of which causes the inflation and tension of the oral lobes. The mechanism of the proboscis will be discussed later (p. (45) 439), but it may be noticed here that in *M. domestica* there is no trace of a trefoil-shaped sac at the base of the oral lobes, and that all the tracheal structures of this the haustellum region are definite annular tracheæ, and therefore incapable of distension.

The posterior thoracic spiracle (figs. 6 and 15, *p.th.*) is triangular in shape and guarded by dendritic processes. It possesses a vestibule which leads into a distributing tracheal sac. The tracheal sacs of this system (fig. 15) have not the extended range of those supplied by the anterior thoracic spiracle, but are confined to the thorax, chiefly in the median and posterior regions which are not aerated to any great

extent by those of the other system. They supply chiefly the large muscles of the thorax. Laterally a series of sacs (*l.th.s.*) extends antero-dorsally in an oblique direction, external to the sterno-dorsales muscles to the humeral region. From the first of these sacs a large number of tracheal twigs arise and supply the muscles of the wing and the anterior sterno-dorsales muscles. Ventral to this sac a large sac (*m.v.s.*) penetrates internally between the anterior and median sterno-dorsales muscles and supplies the lower dorsales muscles. From the dorsal side of the distributing sac a number of sacs arise, some of which penetrate between the sterno-dorsales muscles and supply the upper dorsales muscles. A more posterior set supplies the posterior regions of the dorsales muscles, ramifying between them in a very extensive manner, some ultimately terminating in the tracheal sacs beneath the scutum and the scutellar sac (*sc.s.*).

The abdominal spiracles differ in number in the two sexes. In the male there are seven pairs of abdominal spiracles; in the female I have only been able to find five pairs. In both sexes each of the large tergal plates which cover the abdomen has near its lateral margin a small circular spiracle. The first abdominal segment which has fused with the second has a pair of small spiracles (see fig. 8) slightly anterior to those of the second (apparent first) abdominal segment. In addition to these the male possesses two pairs of spiracles in the membrane at the lateral extremities of the rudimentary sixth and seventh abdominal segments (see fig. 5). In the female I have been unable to find any additional spiracles. Each of the abdominal spiracles is provided with a vestibule and atrium which are separated by a valve controlled by a minute chitinous lever. All the spiracles of the abdomen communicate with tracheæ which ramify among the viscera and fat-body; there are no tracheal sacs in connection with these spiracles.



### 5. The Vascular System and Body-cavity.

By the great development of the tracheal sacs in the head, the muscles in the thorax, and the fat-body and air sacs in the abdomen, the hæmoeœlic space in the fly is greatly reduced. The blood is colourless, and is crowded with corpuscles, mostly containing substances of a fatty nature.

The fat-body varies greatly in the extent of its development. In some cases it may almost fill the body-cavity, pushing the intestine back into a postero-dorsal position: this is generally the case in flies before hibernating; in other cases it may be only moderately developed. The fat-body receives a very rich tracheal supply, and stores the products of digestion which are conveyed to it by the blood with which it is bathed. It consists chiefly of very large cells, both uninucleate and multinucleate; the fat-cells of the head are not so large.

The dorsal vessel or heart lies in the pericardial chamber, immediately beneath the dorsal surface. It extends from the posterior end to the anterior end of the abdomen, and four large chambers, corresponding to the four visible segments, and a small anterior chamber can be recognised; the last represents the chamber of the first abdominal segment. The chambers are not separated by septa, but each has a pair of dorso-lateral ostia situated at its posterior end where the alar muscles of the pericardium arise. The walls of the heart are composed of large cells. The pericardium contains fat-cells and tracheæ, and its floor is composed of large cells of a special nature. The alar muscles run laterally in the floor of the pericardium to the sides of the dorsal plates where they are inserted. The anterior end of the heart is continued as a narrow tube (fig. 20, *d.a.*) along the dorsal side of the ventriculus, where it terminates in a mass of cells (*l.g.*), which are usually considered to be of a lymphatic nature.

## 6. The Reproductive System.

The two sexes are slightly different in size, the females being larger than the males; the sexual dimorphism of the width of the frontal region of the head has already been noticed (p. (8) 402). There does not appear to be any great disparity in the numerical proportions of the sexes; near breeding places there is naturally a preponderance of females.

The Female Reproductive Organs.—The generative organs of the female consist of ovaries, spermathecæ or vesiculæ seminales, accessory glands and their ducts.

The ovaries, when containing mature ova, occupy the greater part of the abdominal cavity (fig. 23, *ov.*). They lie ventral to the gut, occupying the whole of the ventral and lateral regions, the gut resting on the V-shaped hollow between them. Each ovary contains about seventy ovarioles, in each of which ova in various stages of development can be seen. The two short thin-walled oviducts (*ov.d.*) unite on the ventral side of the abdomen to form the common oviduct (*c.o.d.*). The walls of the common oviduct are muscular, and when the ovipositor is in a state of rest, retracted into the abdominal cavity, the oviduct curves forwards and dorsally to enter the ovipositor (*ov.p.*) ventral to the rectum (*rect.*). Here it swells slightly to form a sacculus (fig. 26, *sac.*) which leads into the muscular vagina (*vag.*). The vagina opens into the ventral side of the ovipositor immediately behind the sub-anal plate.

The spermathecæ (*sp.*) or vesiculæ seminales are three in number, two on the left side, and a single one on the right. Each consists of a small, black, oviform, chitinous capsule, the lower half of which is surrounded by a follicular investment continuous with the cellular wall of the duct, the whole having the appearance of an acorn with a long stalk. The ducts of the spermathecæ are lined by a thin chitinous intima continuous with the chitinous capsule, and they open at the posterior end of the sacculus on the dorsal side.

There is a single pair of accessory glands (*ac.g.*), which are fairly long, and on nearing the vagina they become narrower to form a slender duct, which opens on the dorsal side of the vagina immediately behind the ducts of the spermathecae. The accessory glands are closely united with the fat-body. They probably secrete the adhesive fluid which covers the eggs when they are laid, and causes them to adhere to each other and to the material upon which they are deposited. Behind the accessory glands there is a pair of thin-walled transparent vesicles (*tasche dell'ovidutto* of Berlese), which I propose to name the accessory copulatory vesicles (*a.c.v.*) on account of the part they take in ensuring firm coitus with the male during copulation, during which process they expand to a much greater extent.

The ovipositor (fig. 8). The terminal abdominal segments of the female are much reduced to form a tubular ovipositor, the chitinous sclerites being reduced to form slender chitinous rods. When extended it equals the abdomen in length. It is composed of segments vi, vii, viii, and ix, each being separated from the adjacent segments by an extensible inter-segmental membrane, which is covered with fine spines. When the ovipositor is retracted (fig. 23, *orp.*) it lies in the interior of the posterior end of the abdomen, the segments being telescoped the one within the other, so that only the terminal tubercles are visible from the exterior. The dorsal arch of the sixth abdominal segment is reduced to a  $\Lambda$ -shaped sclerite (vi, *d.*), lying on the dorsal side of the segment. The ventral arch of this segment is reduced to a slender chitinous rod (vi, *v.*) in the mid-ventral line. The dorsal arch of the seventh segment is represented by two slightly-curved sclerites (vii, *d.*), with their concave faces opposite; the ventral arch (vii, *v.*) is similar to that of the sixth segment. At the junction of the posterior ends of the sixth and seventh segments with the inter-segmental membranes succeeding them there are several setose tubercles arranged more or less in pairs, but they vary in development in different individuals. The dorsal arch of the eighth

segment consists of two parallel and slender sclerites (viii, *d.*), not so narrow as those of the two preceding segments. A pair of slender sclerites (viii, *v.*) also represents the ventral arch. The terminal anal segment, which I consider represents the reduced ninth segment, has a dorsal chitinous sclerite, the sub-anal plate (*su.p.*), which is triangular in shape, and a ventral sub-anal plate of the same shape. The female genital aperture is situated at the anterior end of the latter plate, between the eighth and anal (ninth) segments. A pair of terminal setose tubercles is situated laterally at the apex of the anal segment.

The Male Reproductive Organs.—The male reproductive organs (fig. 24) are situated ventral to the alimentary canal, and lie within the fifth abdominal segment. They consist of a pair of testes, vasa deferentia, ejaculatory duct and sac, and the terminal penis. There are no accessory genital glands in the male.

The testes (*te.*) are a pair of brown pyriform bodies, with their long axes placed transversely, and their pointed ends facing. In young males they have a bright red appearance. They are covered with a follicular investment of cells, which varies in thickness apparently according to age. The thin brown chitinous capsules contain the developing spermatozoa. The pointed end of each testis is continued as a fine vas deferens (*v.d.*), which meets that of the other testis in the median line, where they open into the common ejaculatory duct (*d.e.*). This runs forwards for a short distance, and then bends to the left ventrally, and, after several convolutions on the left ventral side of the abdomen, the duct narrows considerably, forming a narrow ejaculatory duct. This crosses over the dorsal side of the rectum to the right side, where it runs forwards for a short distance and then curves back in the median ventral line, opening into a pyriform ejaculatory sac (*e.s.*). The walls of this ejaculatory sac are muscular, longitudinal muscles, giving the walls a striated appearance. It contains a phylliform, chitinous sclerite—the ejaculatory apodeme (*e.a.*), which has a short handle at the broad end.

This sclerite is, no doubt, of great assistance in propelling the seminal fluid along the ejaculatory duct during copulation. A short distance behind the ejaculatory sac the duct opens into the penis.

The Male Gonapophyses.—The extremity of the abdomen in the male (fig. 10) has undergone considerable modification in the formation of the external genitalia. The visible portion of the abdomen, as seen from above, consists of the first five abdominal segments; the remaining three segments are slightly withdrawn into the fifth segment, and, on looking at the abdomen from the posterior end, only the terminal segment, the eighth, surrounding the anus, can be seen. The sixth and seventh segments have been greatly reduced. The sternal portion of the fifth segment consists of a cordiform sclerite (*V.v.*), the apex of which is directed forwards, and each of the lateral margins of the base is produced to form a short process, swollen at the tip—these lateral processes form the primary forceps (*pf.*), and lie at each side of the aperture of the male genital atrium (*g.a.*), of which the posterior edge of the sclerite forms the lower or anterior lip. The dorsal plates of the sixth and seventh segments lie on the membrane, which is tucked underneath the posterior edge of the fourth abdominal segment. The dorsal plate of the sixth segment (*vi, d.*) is a narrow, transverse sclerite; its lateral edges, which do not extend down the sides, are slightly produced anteriorly. The ventral plate of the sixth segment (*vi, v.*) is asymmetrical, and, with the dorsal plate of the seventh segment, produces a pronounced asymmetry of the posterior end of the male abdomen. It consists of a spatulate plate on the left side, the anterior or ventral side of which is produced into a narrow bar extending across the ventral side of the aperture of the genital atrium, its distal extremity bifurcating. The dorsal plate of the seventh segment (*vii, d.*) is asymmetrical. It consists of a narrow sclerite, which, on the dorsal side, is similar to the sixth dorsal plate, but the left side (see fig. 5) extends down the side, and broadens out into a somewhat



triangular-shaped area; the anterior edge of this is incised, and receives the seventh spiracle (vii, *a.sp.*); the ventral edge is internal to the spatulate portion of the sixth ventral plate. The ventral arch of the seventh sclerite has been completely withdrawn into the abdomen, and consists of a pair of curved sclerites (fig. 9, vii, *v.*), somewhat rhomboidal in shape, lying dorsal to the fifth ventral arch and ventral to the penis (*P.*); they form the secondary forceps. Their lateral edges, which are thickened articulate with the alar processes of the body of the penis (*c.pe.*), and with the dorsal arch of the eighth abdominal segment (viii, *d.*). Their inner edges are curved, and almost meet in the mid-ventral line. The dorsal arch of the eighth and last abdominal segment (viii, *d.*) forms the apex of the abdomen. It consists of a strongly convex sclerite, deeply incised on the ventral side; in this incision the vertical slit-like anus (fig. 10, *an.*) lies. The ventral portion of the segment is completed by a pair of convex sclerites (viii, *v.*), which are united in the mid-ventral line, forming the ventral border of the anal membrane and the dorsal side of the entrance to the genital atrium.

All the sclerites of the posterior segments except the sixth and seventh are setose.

Berlese (1902) in his account of the copulation of the House-fly describes the genitalia. From his account of the male genitalia he appears to have missed the narrow dorsal arch of the sixth segment, or, what is very probable, he may have mistaken it for the fifth dorsal arch, as he terms the seventh dorsal arch the sixth, and describes what I have called the ventral arch of the seventh as the dorsal arch of that segment. This mistake in nomenclature has probably arisen from the fact that he considered the visible portion of the abdomen as consisting of four segments instead of five, in which case the narrow dorsal arch of the sixth segment would naturally be taken for that of the fifth.<sup>1</sup>

<sup>1</sup> Berlese describes a sinistral asymmetry of the posterior segments, but his figures show a dextral asymmetry, a mistake probably in the reproduction of his figures which has escaped the author's notice.

The penis (figs. 7 and 9) lies internally on the ventral side of the abdomen, dorsal to the ventral arches of the fifth and seventh segments. It is composed of several sclerites. A median sclerite (*c.pe.*), the anterior and ventral edge of which is roughly semicircular in outline, forms the body of the penis. This is produced laterally to form two alar processes; at the bases of these processes the lateral extremities of the dorsal arch of the eighth segment articulate with the body of the penis; the extremities of the processes are attached to the lateral extremities of the ventral sclerites of the seventh segment, the secondary forceps. The penis proper consists of a hollow cylindrical tube, the theca, which receives the ejaculatory duct. The theca articulates with the body of the penis by means of a pair of small chitinous nodules ("cornetti" of Berlese); posterior to the attachment the theca is constricted slightly. Below the aperture for the entrance of the ejaculatory duct, the theca is produced into a ventrally directed curved process, the inferior apophysis (*i.ap.*); above the aperture a short cylindrical process, the superior apophysis (*s.ap.*), arises. The anterior end of the theca is continued as a slightly inflated hyaline structure, the glans (*p.gl.*), at the curved extremity of which the ejaculatory duct opens.

## V. THE INTERNAL STRUCTURE OF THE HEAD.

The skeletal framework and tracheal system of the head have already been described. It remains, therefore, to give an account of the musculature of the head and pharynx, and also an account of the oral lobes.

The posterior region of the head (fig. 1) not occupied by tracheal sacs is usually filled up with small multinucleate fat-cells (*f.c.*), which are also occasionally found in the proboscis. The frontal sac or ptilinium (*Pt.*) fills up the anterior portion of the head not occupied by air-sacs. Its crescentic opening, the lunule, has already been described. It is attached to the



wall of the cephalic capsule by muscles which vary considerably in the extent of their development. In recently emerged flies the muscle-supply of the ptilinum is considerable, as they have served to retract the sac after it has been inflated to assist the exclusion of the imago, but in older specimens it becomes less. The walls of the ptilinum are muscular and lined by a chitinous intima covered with small broad spines.

The Musculature of the Proboscis.—The chief muscles controlling the movements of the pharynx and proboscis are these:

The Dilators of the Pharynx (figs. 1 and 2, *d.ph.*).—This pair of muscles occupies the interior of the fulcrum. Each muscle is attached to the antero-lateral regions of the fulcrum and inserted into the dorsal plate of the pharynx (*r.p.*). These muscles are the chief agents in pumping the liquid food into the œsophagus, and in drawing it up through the pharyngeal tube.

The Retractors of the Fulcrum (fig. 1, *r.f.*).—These muscles are attached to the internal anterior edges of the genæ, and are inserted into the posterior cornua (*p.c.*) of the fulcrum. Their contraction causes the rotation of the fulcrum on the epistome as a hinge in the retraction of the proboscis.

The Retractors of the Haustellum (*r.h.*).—These muscles have their origin on the dorso-lateral regions of the occiput. They are long and narrow, and running on each side of the common salivary duct are inserted into the dorsal margin of the theca.

The Retractors of the Rostrum (*r.r.*).—This pair of muscles has its origin at the sides of the occipital foramen, and is inserted into the posterior side of the membranous rostrum about half-way down its length. In the retraction of the proboscis these muscles draw in the rostrum.

The last two pairs of muscles acting together assist in the retraction of the whole proboscis.

The Flexors of the Haustellum (*f.h.*) have their origin close to that of the retractors of the rostrum at the

sides of the occipital foramen. They are inserted into the base of the labral apodeme (*ap.*), and serve to flex the haustellum on to the anterior face of the rostrum.

The Extensors of the Haustellum (*ex.h.*).—Each of these muscles arises from the distal cornu of the fulcrum, and is inserted into the head of the labral apodeme.

The Accessory Flexors of the Haustellum (*a.f.h.*) are attached to the lower (distal) anterior margin of the fulcrum, and inserted with the extensors into the head of the labral apodeme.

The Flexors of the Labium-epipharynx (*f.l.*).—These muscles have their origin on the anterior and upper edge of the fulcrum, and are inserted into the proximal end of the labium-epipharynx. The first pair of the last three sets of muscles serve to extend the haustellum in the extension of the proboscis, and the remaining two pairs assist in the retraction of the proboscis by flexing the haustellum on to the rostrum.

A pair of very fine muscles (*s.m.*) have their origin at the base of and internal to the posterior cornua of the fulcrum. They are inserted into the dorsal side of a small valve (*s.v.*) on the common salivary duct which regulates the flow of the secretion of the lingual salivary glands.

The muscles of the haustellum are—

The Retractors of the Furca (*r.fu.*).—A pair of muscles having their origin on the upper part of the theca. Each is inserted along the upper proximal half of the lateral process of the furca. When the muscles contract the lateral processes of the furca, which, in a state of repose are brought together by the elasticity of the ventral cornua of the theca, are diverged, and thus cause the divergence and opening of the oral lobes.

The Retractors of the Discal Sclerites (*r.d.s.*).—These muscles have their origin on the lateral edges of the upper part of the theca, and are inserted upon the sides of the discal sclerites. They work together with the retractors

of the furca, their contraction causing the divergence of the discal sclerites, and the consequent opening of the oral pit.

The Dilators of the Labium-hypopharynx (*dil.*).—These fan-shaped muscles arise in the middle region of the theca on either side the median line, and diverging are inserted in the lateral edges of the labium-hypopharyngeal sclerite. By their contraction they will widen the channel of the labium-hypopharynx.

The Dilators of the Labium-epipharynx (*dil.*).—These form a series of short muscles attached to the anterior and posterior walls of the labium-epipharynx. The size of the pharyngeal channel will be regulated by these muscles.

The Oral Lobes.—The external structure of the oral lobes has already been described. Their internal structure and histology will be given here, as it seemed preferable to do so rather than postpone it to a future communication.

The setigerous cuticle and the pseudo-tracheæ lie on a hypodermis of cubical cells (fig. 18, *hy.*). Beneath the hypodermis of the aboral surface is another layer of cells containing a large amount of dark pigment. Each of the large marginal sensory bristles (*g.s.*) of the aboral surface has a fine channel running down the whole length of the seta. This channel communicates with the cavity of a pyriform mass of nerve-end cells (*s.p.*), consisting of five or six cells. These masses of cells occupy a large part of the interior of the oral lobes. As these gustatory bristles are exposed and directed ventrally when the proboscis is retracted, they may assist the fly in testing the nature of its food before extending its proboscis. On the oral side of the oral lobes the nipple-like gustatory papillæ (figs 1 and 18, *gp.*) have already been described. The aperture at the end of the papilla leads into a fine duct, which ends in a pyriform sensory bulb (*s.g.p.*). The tracheæ (*tr.*) can be seen running through the cells, some of which contain several nuclei, and from their appearance are probably derived from the fat-body. No tracheal sacs could be found either in the oral lobes or at their bases, but the annular tracheæ are continuous with those of the proboscis. The

hæmocœl of the oral lobes is well developed. This supports the view set forth by Kraepelin, and with which I agree that the inflation of the oral lobes is due to the blood. I consider that the extension of the proboscis is due to the inflation of the tracheal sacs of the head. The proboscis having been protruded the oral lobes are then diverged by the contraction of the retractor muscles of the furca and discal sclerites, and distended by the inrush of blood which keeps them turgid, and causes the openings into the pseudo-tracheal channels to remain open.

The Labial Salivary Glands (figs. 19 and 1, *lb.sl.*).—These salivary glands lie in the haustellum at the base of the oral lobes. The glands, which are spherical in shape, are composed of a large number of gland cells somewhat triangular in shape. Each gland cell is  $40\mu$  in size, and possesses a large nucleus ( $12\mu$ ), and internal to this a permanent circular vacuole (*vac.*), which is  $16\mu$  in size, and is lined by a thin chitinous intima. The duct of each gland cell opens into the side of the vacuole (*od.*). The ducts (*ic.d.*) are intracellular, and run from the centre of the gland, some of them uniting; to form a number of fine ducts on the ventral sides of the discal sclerites, which unite and open into the oral pits by a median pair of pores. Kraepelin, in his description of the proboscis of the blowfly, described the labial glands and their ducts (but not their histology) of that insect, his description being similar to the condition I find in *M. domestica*. Lowne, however, states that in the blowfly he traced the ducts of the gland cells through the oral lobes to the apertures of the gustatory papillæ, which he regarded therefore as the apertures of the labial salivary glands.

The secretion of the labial salivary gland serves to keep the surface of the oral lobes moist.

## VI. SUMMARY.

1. The exoskeleton of the head capsule and of the pharynx is described in detail; the relations of the parts in the terms

generally employed by dipterologists to the morphological divisions of the insect head capsule are shown. On morphological grounds, the view that the distal portion of the proboscis represents the modified second maxillæ or labium is adopted, as opposed to that of a first maxillary derivation put forward by Lowne for the blowfly.

2. After a detailed description of the external and internal skeletal structures of the thorax, the neurulation of the wings is described in the terms proposed by Comstock and Needham in their valuable memoir; and to facilitate their more general adoption for the wings of the Muscidae and other Diptera, a comparison is made between their nomenclature and the several systems employed in describing the muscid wing.

3. The abdomen is shown to consist of eight segments in the male and nine in the female, in both cases the first five segments form the visible portion of the abdomen; the external genitalia of the two sexes are described under another section.

4. As the muscular system does not differ from that of *Volucella* described by Kunckel d'Herculais and the blowfly described by Hammond and Lowne, it is briefly described. The cephalic muscles, however, are fully described in the detailed description of the head (V).

5. The nervous system, which is of the normal muscid type, is described, but for the sake of clearness a very detailed description of the composition of the cephalic ganglion is not given. The structure of the optic tract is similar to that of the blowfly as described by Hickson. The structure of the thoracic nerve-centre is found to differ slightly from that of the blowfly as described by Lowne.

6. The alimentary canal is similar in its structure to those of *Stomoxys* and *Glossina*, only differing in a few details. The mesenteric region, which is represented by the ventriculus or chyle, stomach, and proximal intestine, is well developed. The lingual salivary glands, rectal glands, and



Malpighian tubes are described; the function of the rectal glands is believed to be of an excretory nature.

7. As the tracheal systems of the Diptera have not received much attention a detailed account of the tracheal system is given. There are two thoracic spiracles, the first of which supplies the whole of the head, the anterior and median regions of the thorax and the three pairs of legs, and by means of a pair of large abdominal air-sacs a large part of the viscera. The posterior thoracic spiracle supplies the muscles of the median and posterior region of the thorax, especially the large dorsales muscles. There are seven pairs of abdominal spiracles in the male and five pairs in the female all of which are connected with tracheæ only.

8. The dorsal vessel or heart is found to consist of five incomplete chambers, each with a pair of ostia. The anterior end is continued forwards along the dorsal side of the ventriculus, and terminates in a glandular mass in the anterior margin of the proventriculus.

9. The reproductive organs of the male are simple, consisting of a pair of testes, vasa deferentia, and common ejaculatory duct; there are no accessory glands such as are found in many other Diptera. The terminal abdominal segments of the male exhibit a sinistral asymmetry.

The ovaries of the female, when mature, occupy the greater portion of the abdominal cavity. There are a pair of accessory glands (probably of a "gum" or "glue" nature), three spermathecae, and a pair of vesicles used during copulation. The ovipositor is about as long as the abdomen, and is composed of segments six to nine.

10. The musculature of the head is described in detail, and it is found that the House-fly agrees with the blowfly in the number and relations of its cephalic muscles, though in a few cases the attachments are slightly different. In the haustellum and oral lobes of the House-fly no tracheal sacs similar to those described and figured by Lowne for the blowfly occur, but only annulated tracheæ are found, and, as these are incapable of distension, the view that the oral lobes are

distended by the action of inflated air cannot be held. The extension of the proboscis I believe is due to the inflation of the tracheal sacs of the head and rostrum, and I agree with Kraepelin that the distension of the oral lobes is effected by blood-pressure.

Two kinds of gustatory sense-organs are found on the margin of the aboral and on the oral surfaces respectively. The latter were described in the blowfly by Lowne as the openings of the duets of the labial salivary glands, but Kraepelin's correct description of their structure in the blowfly is confirmed by this study of the House-fly. The labial salivary glands are described in detail. They consist of large cells containing permanent vacuoles, which communicated with intracellular ducts. These open by a pair of pores into the oral pits, the secretions of the glands serving to keep the surface of the oral lobes moist.

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## EXPLANATION OF PLATES 22—26,

Illustrating Mr. C. Gordon Hewitt’s paper on “The Structure, Development, and Bionomics of the House-fly (*Musca domestica*, Linn.). Part I. Anatomy of the Fly.”

### PLATE 22.

- FIG. 1.—*Musca domestica*. Female.  
 FIG. 2.—*Anthomyia radicum*. Female.  
 FIG. 3.—*Homalomyia canicularis*. Male.  
 FIG. 4.—*Stomoxys calcitrans*. Female. The halteres of this species have been drawn too far back, and in this and the other species the nervures of the wings have been made thicker than they naturally are.  
 These figures are not drawn to the same scale.

### PLATE 23.

FIG 1.—Interior of the head of *M. domestica*. In this figure the left side of the head capsule and of the proboscis have been removed and the compound eye of the same side, leaving the optic ganglion (periopticon). All the tracheal structures have been omitted.

*a.c.* Anterior cornu of fulcrum. *a.f.h.* Accessory flexor muscles of haustellum. *ap.* Apodeme of labrum. *an.n.* Antennal nerve. *C.G.* Cephalic ganglion. *di.l.* Dilator muscles of labium hypopharynx. *d.ph.* Dilator muscles of pharynx. *d.s.* Discal sclerite. *ex.h.* Extensor muscle of haustellum. *F.* Fulcrum. *f.* Furca. *f.c.* Fat-cells. *f.h.* Flexor muscle of haustellum. *f.l.* Flexor muscle of labrum-epipharynx. *g.p.* Gustatory papillæ of oral lobes. *k.* Hyoid sclerite of pharynx. *lb.n.* Labial nerve. *lb.sl.* Labial salivary gland. *l.hp.* Labium-hypopharynx. *l.ep.* Labrum-epipharynx. *m.x.p.* Maxillary palp. *œs.* Oesophagus. *oc.n.* Ocellar nerve. *ph.n.* Pharyngeal nerve. *p.c.* Posterior cornu of fulcrum. *P.O.* Periopticon. *ps.* Pseudotrachea. *Pl.* Ptilinum. *r.d.s.* Retractor muscles of the discal

sclerites. *r.f.* Retractor muscle of the fulcrum. *r.fu.* Retractor muscle of the furca. *r.h.* Retractor muscle of haustellum. *r.r.* Retractor muscle of rostrum. *S.O.* Sub-œsophageal ganglion. *sal.d.* Common duct of the lingual salivary glands. *s.v.* Valve of the common salivary duct. *s.m.* Muscle controlling the valve of salivary duct. *th.* Theca.

FIG. 2.—Transverse section through the lower portion of the head-capsule, showing the muscles and tracheal sacs in this region and the fulcrum in section. (Camera lucida drawing.)

*bp.* Floor of pharynx. *r.p.* Roof of pharynx. *tr.s.* Tracheal sac. Other lettering as in Fig. 1.

FIG. 3.—Transverse section through the lower half of the haustellum, where the hypopharynx (*hp.*) has become free from the labium. (Camera lucida drawing.)

*di.l.* Dilator muscles of the labium-epipharynx. *tr.* Trachea. Other lettering as in Fig. 1.

FIG. 4.—Posterior view of the tracheal ducts which supply the cephalic sacs and tracheæ.

*c.tr.* Cervical tracheæ which fuse above the œsophagus on the posterior side of the cephalic ganglion. *l.d.* Lateral duct. *m.d.* Median dorsal duct. *tn.d.* Tentorial tracheal ducts which spread out beneath the cephalic ganglion.

FIG. 5.—Lateral view of the terminal segments of the abdomen of the male after their removal from the fifth segment.

*vi, a.sp.* and *vii, a.sp.* Sixth and seventh abdominal spiracles. Lettering as in Fig. 10.

FIG. 6.—The thorax seen from the left side. The insertions of the larger setæ are shown; for the sake of clearness the sclerites of the wing-base are omitted.

*a.th.* Anterior thoracic spiracle. *ca.* Costa. *cp.* Intermediate coxal plates. *cp', cp''.* Epimera of the meso- and meta-thoracic segments. *eps', eps'', cps''.* Episterna of the pro-, meso-, and meta-thoracic segments. *hal.* Haltere. *hu.* Humerns. *lp.* Lateral plate of mesosternum. *lp.sc.* Lateral plate of postscutellum. *mph.* Mesophragma. *mpsc.* Median plate of postscutellum. *mn.* Metanotum. *ms.* Mesosternum. *mts.* Metasternum. *p.th.* Posterior thoracic spiracle. *pt.* Parapterm. *pr.n.* Pronotum. *prs.* Pre-scutum of mesothorax. *sc.* Scutum. *scvl.* Scutellum.

FIG. 7.—Penis seen from the right side after it has been removed from within the terminal abdominal segments.

*i.ap.* Inferior apophysis. *th.p.* Theca of penis. *p.gl.* Glans. *s.ap.* Superior apophysis. Other lettering as in Fig. 9, etc.

FIG. 8.—Abdomen of female showing the extended ovipositor.

*V, d. to ix, d.* Fifth to ninth dorsal arches or plates of the abdomen. *V, v.*

to viii, *v*. Fifth to eighth ventral plates or arches. *su.p.* The suranal plate (ninth dorsal arch).

The anus is situated between the two lateral terminal tubercles.

FIG. 9.—Dorsal view of the penis and the ventral half of the terminal abdominal segments. The median portion of the eighth dorsal arch has been removed, leaving the lateral portions attached to the body of the penis (*c.pe.*) and the ventral arch of the seventh segment (vii, *v.*).

Lettering as in Fig. 10.

FIG. 10.—The posterior end of the abdomen of the male seen from behind, showing the pronounced sinistral asymmetry.

*v, d.* to viii, *d.* Fifth to eighth dorsal plates or arches. *v, v.* to viii, *v.* Fifth to eighth ventral plates or arches. *an.* Anus. *g.a.* Aperture of genital atrium. *p.f.* Primary forceps.

#### PLATE 24.

FIG. 11.—Nervous system. The very fine nerve which runs along the dorsal side of the œsophagus to the proventricular ganglion (*Pv.g.*, Fig. 20) has been purposely omitted.

*ab.n.* Abdominal nerve. *ac.ms.* Accessory mesothoracic dorsal nerve. *ac.mt.* Accessory metathoracic dorsal nerve. *cer.n.* Cervical nerves. *cn.* Cephalothoracic nerve cord. *O.P.* Optic peduncle. *pr.cr., ms.cr., mt.cr.* Pro-, meso-, and meta-thoracic crural nerves. *pr.d., ms.d., mt.d.* Pro-, meso-, and meta-thoracic dorsal nerves.

FIG. 12.—Thoracic compound ganglia. Left aspect.

Lettering as in Figs. 11 and 14.

FIG. 13.—The tracheal sacs supplied by the anterior thoracic spiracle (*a.th.*). In this figure the tracheal sacs supplied by the posterior thoracic spiracle and the sterno-dorsales muscles of the left side have been removed. The left side of the head and proboscis have also been removed. The first abdominal segment has been removed to show the large abdominal air sacs (*ab.s.*) and an abdominal trachea which is supplied by the second abdominal spiracle (*a.sp.*).

*a.c.s.* Anterior cephalic sac. *a.v.s.* Anterior ventral thoracic sac. *c.tr.* Cervical tracheal duct. *d.c.* Dorsal cephalic sac. *do.* Dorsales muscles. *H.* Haustellum. *l.tr.s.* Longitudinal tracheal sac. *p.c.s.* Posterior cephalic tracheal sacs. *p.v.s.* Posterior ventral thoracic sac. *p.op.* Periopticum. *Ros.* Rostrum. *v.c.s.* Ventral cephalic sac.

FIG. 14.—Thoracic compound ganglion after the removal of the cortex. Seen from the ventral side. This and Fig. 12 were drawn from models reconstructed from sections.

*Pr.G., Ms.G., Mt.G.* Pro-, meso-, and meta-thoracic ganglia. *A.G.* Abdominal ganglion. Other lettering as in Fig. 11.

FIG. 15.—The tracheal sacs supplied by the posterior thoracic spiracle.

In this figure the left side of the thorax has been removed, together with the wing muscles and the posterior sterno-dorsales. It must be imagined that this figure is superimposed on Fig. 13.

*do.* Dorsales. *l.th.s.* Lateral thoracic sac. *m.v.s.* Median ventral sac. *v.th.* Posterior thoracic spiracle. *sc.s.* Scutellar sac. *st.do.* Sterno-dorsales.

FIG. 16.—Wing. The nervures are drawn slightly thicker than they naturally are.

*an.* Anal lobe. *al.* Alula. *as.* Antisquama. *A.* Anal cell. *A<sub>1</sub>.* Anal nervure. *Cu.* Cubital cell. *1 Cu.* First cubital cell. *cu-a.* Cubito-anal transverse nervure. *C<sub>1</sub>.* Costa. *C.* Costal cell. *1 C.* First costal cell. *M.* Medial cell. *m.cu.* Medio-cubital transverse nervure. *m.* Medial transverse nervure. *2 M<sup>1</sup>, 2 M<sup>2</sup>.* First and second second medial cells. *M 1+2.* Medial longitudinal nervure. *M 3+Cu.* Medio-cubital longitudinal nervure. *R.* Radial cell. *R 1 to R 4+5.* Radial longitudinal nervures. *Sc.* Subcostal cell. *Sc<sub>1</sub>.* Subcosta.

## PLATE 25.

FIG. 17.—The alimentary canal as it is seen on dissection from the dorsal side. The malpighian tubes have been omitted, and also the distal portion of the lingual salivary gland (*s.lg.*) of the right side. The duct of the crop (*Cr.*) is shown by the dotted line beneath the proventriculus (*Pv.*) and ventriculus (*Ven.*).

*p.int.* Proximal intestine. *d.int.* Distal intestine. *rect.* Rectum.

FIG. 18.—Portion of a transverse section of the oral lobes, showing the two types of gustatory sense organ, etc.

*g.s.* Gustatory seta. *g.p.* Gustatory papilla. *hy.* Hypodermis under which lies a pigmented layer. *p.s.* Pseudo-trachea in section. *s.g.p.* Sensory bulb of gustatory papilla. *sp.* Sensory bulb of gustatory seta. *tr.* Trachea.

FIG. 19.—Transverse section of labial salivary gland, to show the structure of the gland cells (*g.c.*). (Camera lucida drawing.)

*hy.* Hypodermis. *ic.d.* Intracellular duct. *p.s.* Pseudo-trachea. *od.* Opening of intracellular duct into the permanent vacuole (*vac.*) of the gland cell.

FIG. 20.—Section through the proventriculus and the anterior end of the ventriculus, to show the structure of the proventricular plug (*Pv.p.*) and the ducts of the œsophagus (*œs.*) and crop (*d.cr.*). (Camera lucida drawing.)

FIG. 21.—The posterior region of the alimentary canal, to show the rectal glands (*rect.gl.*) with their tracheal supply, the origin of the malpighian tubes (*malp.*), and the position of the rectal valve indicated at  $\times$ .

FIG. 22.—Transverse section of the lingual salivary gland, showing the fibrillar character of the gland cells.  $\times 220$ . (Camera lucida drawing.)

PLATE 26.

FIG. 23.—Female reproductive organs in situ; the left ovary and the viscera have been removed. The ovipositor (*ovp.*) is shown retracted, in which state the common oviduct (*c.o.d.*) is doubled back.

*ac.g.* Accessory gland. *a.c.v.* Accessory copulatory vesicle. *ov.* Ovary composed of about seventy ovarioles, and containing ova in various stages of development. *ov.d.* Oviduct. *retr.m.* Retractor muscles of the ovipositor. *Sp.* Spermathecae or vesiculæ seminales.

FIG. 24.—The male reproductive organs. They have been slightly spread out, and the rectum (*rect.*) has been turned over to the right side.

*d.e.* Ejaculatory duct. *e.a.* Ejaculatory apodeme. *e.s.* Ejaculatory sac. *te.* Testis. *v.d.* Vas deferens.

FIG. 25.—Vertical section of one of the rectal glands, to show its structure.  $\times 56$ . (Camera lucida drawing.)

*sh.* Perforate chitinous sheath. *r.gl.* Gland cell. *tr.* Trachea.

FIG. 26.—Terminal region of the female reproductive organs, showing the accessory glands, etc.

*sac.* Sacculus. *vag.* The muscular vagina which evaginates during copulation; a pair of retractor muscles are shown. Other lettering as in Fig. 23.



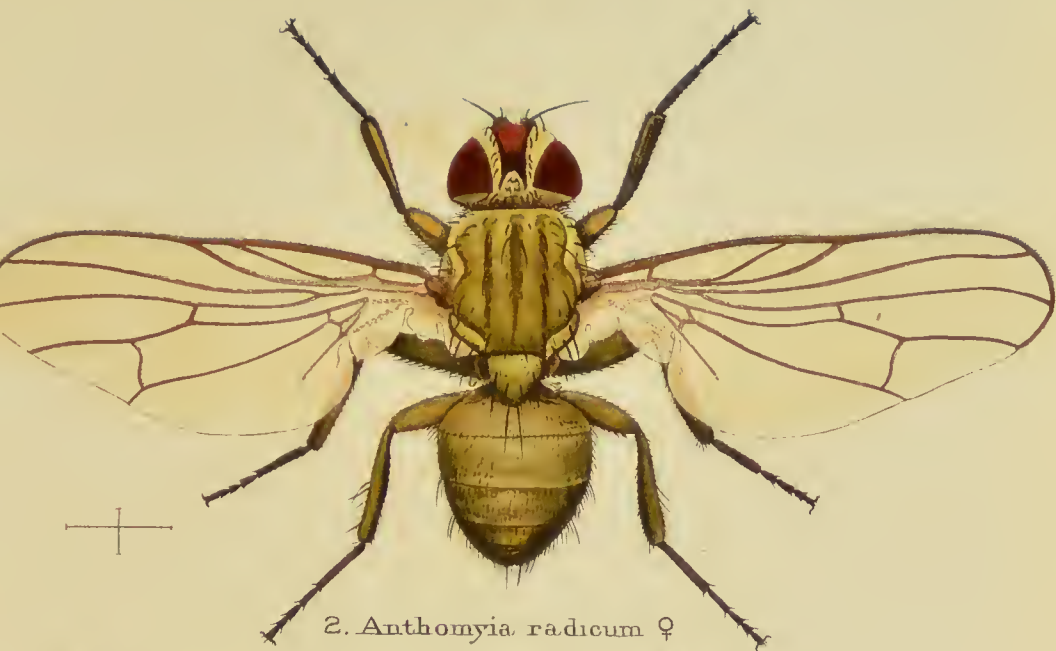




1. *Musca domestica* ♀



3. *Homalomyia canicularis* ♂



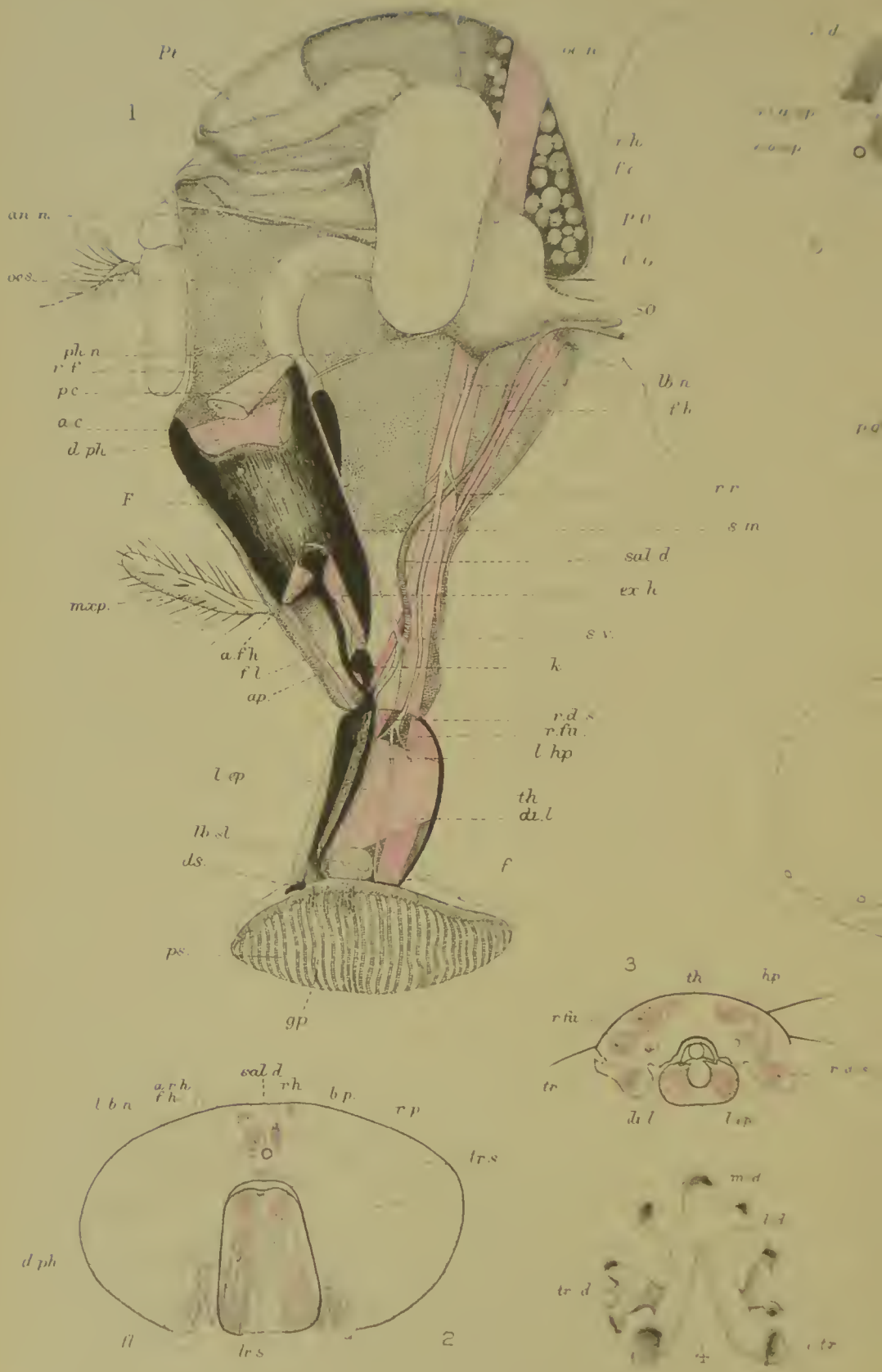
2. *Anthomyia radicum* ♀



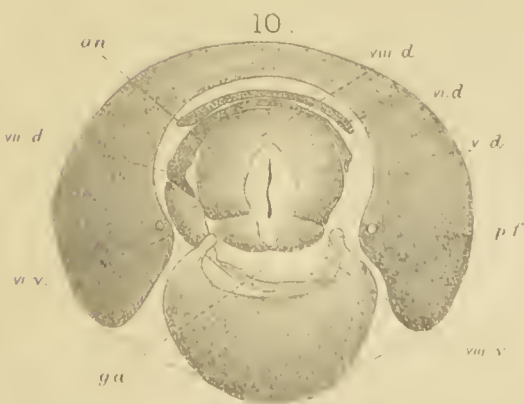
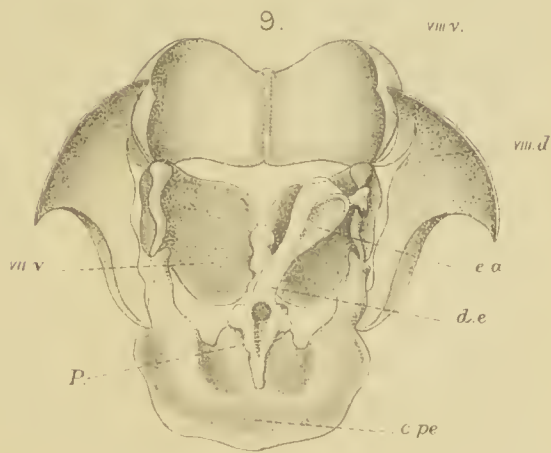
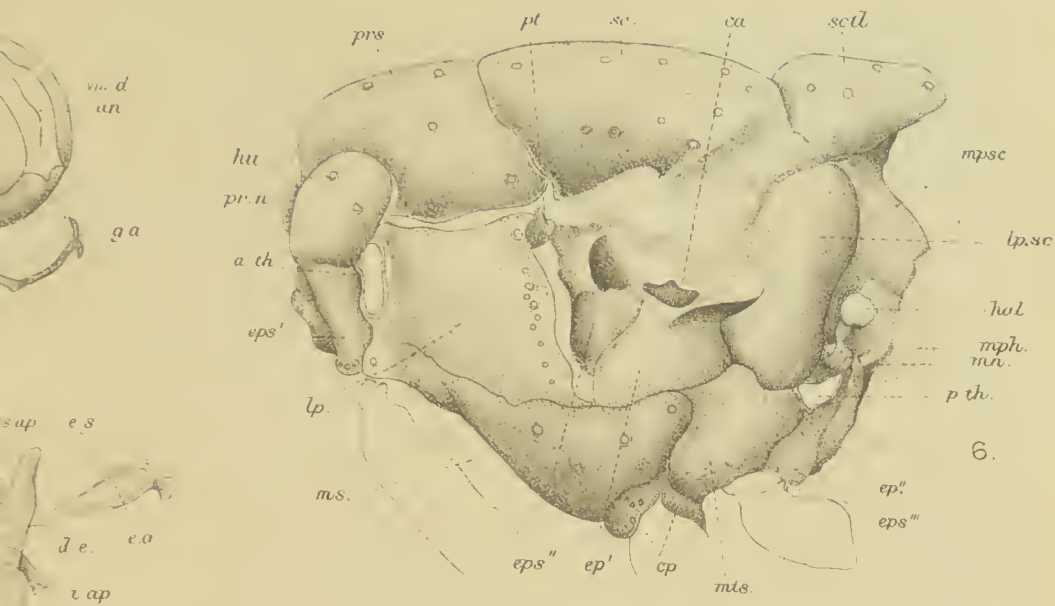
4. *Stomoxys calcitrans* ♀





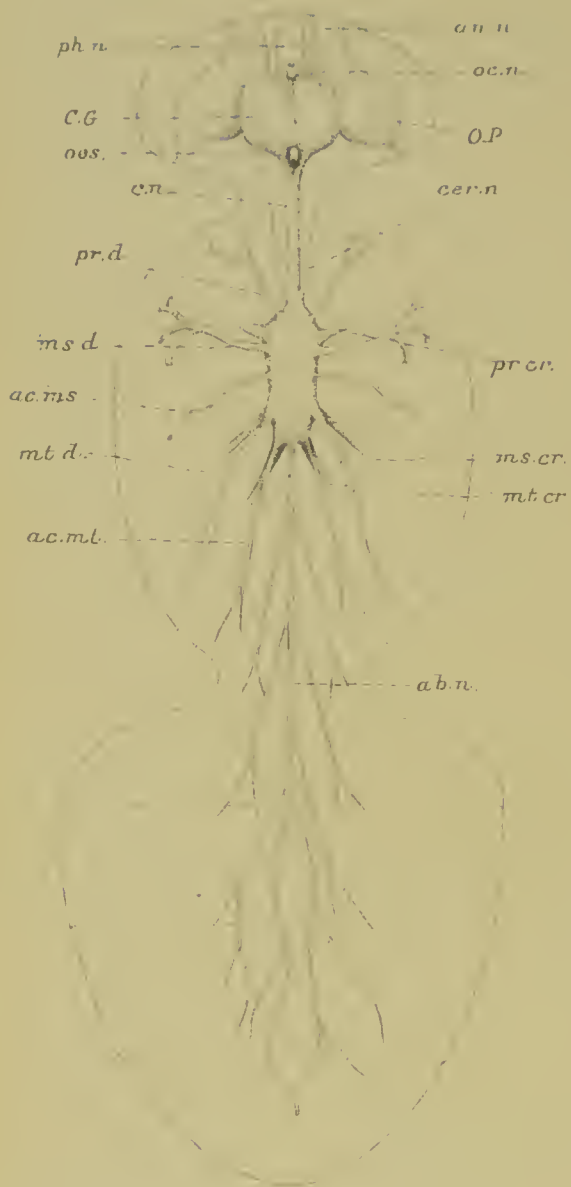




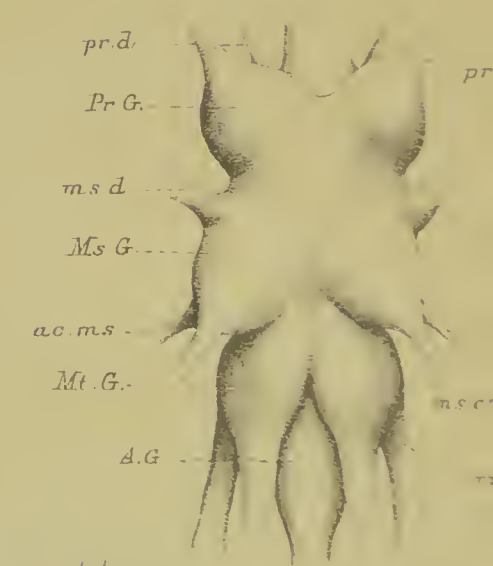
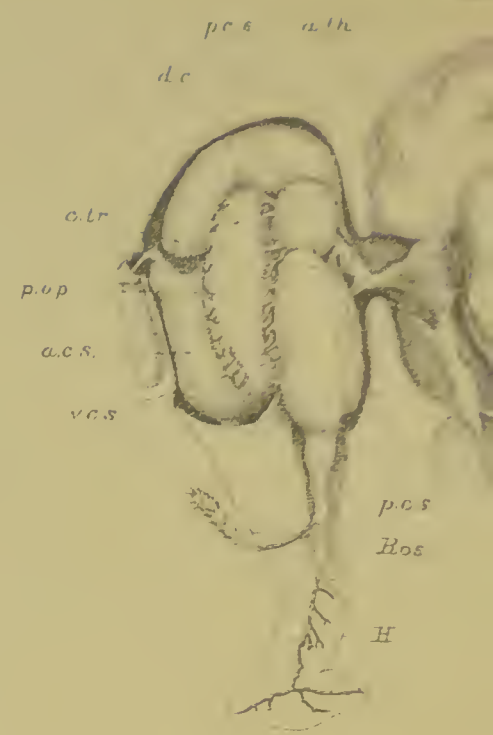




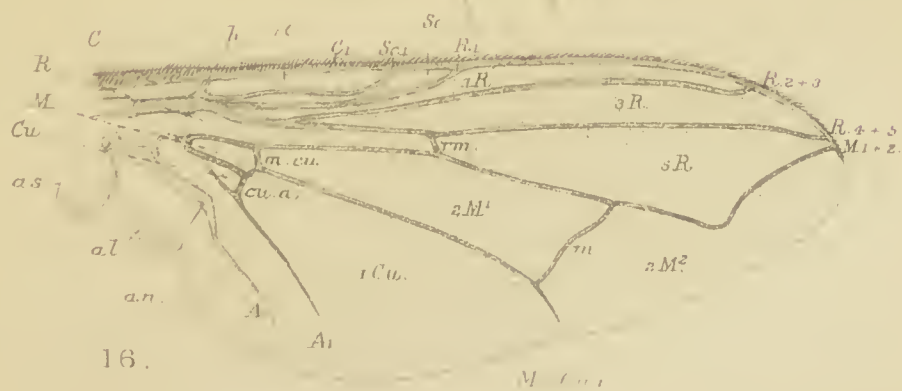
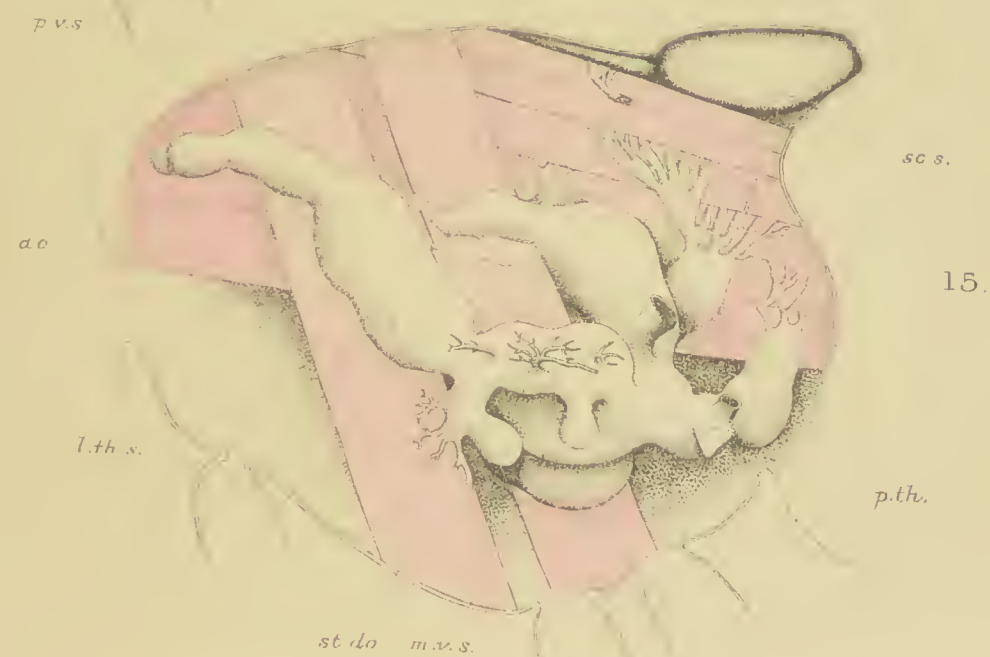
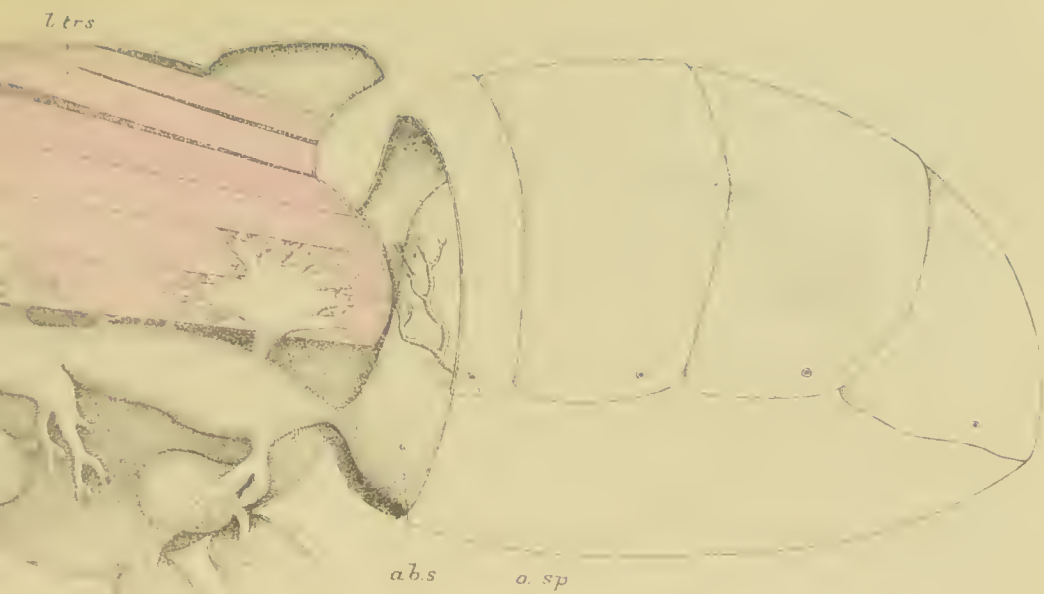




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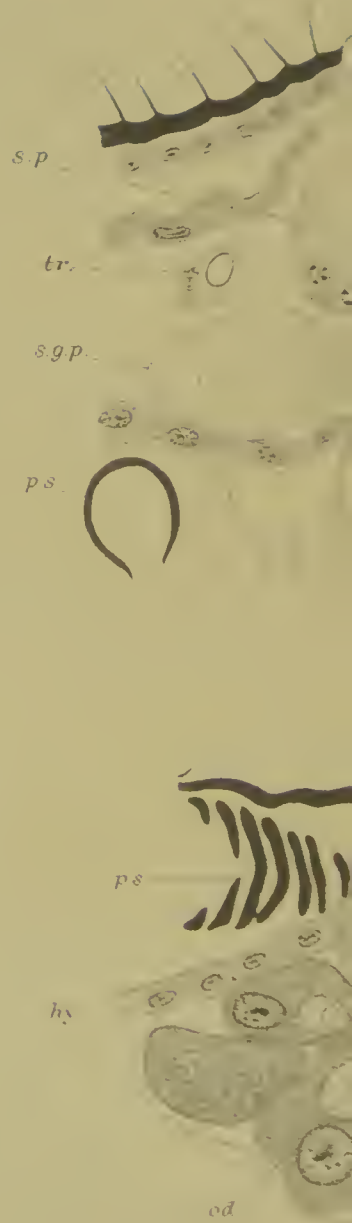
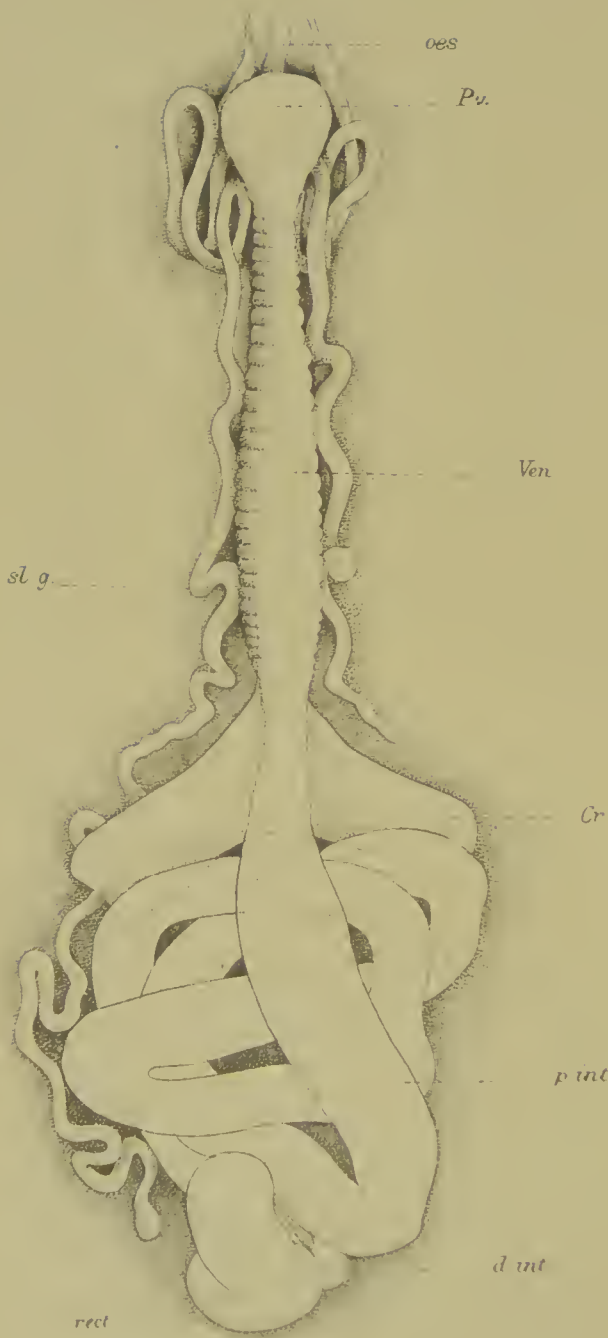
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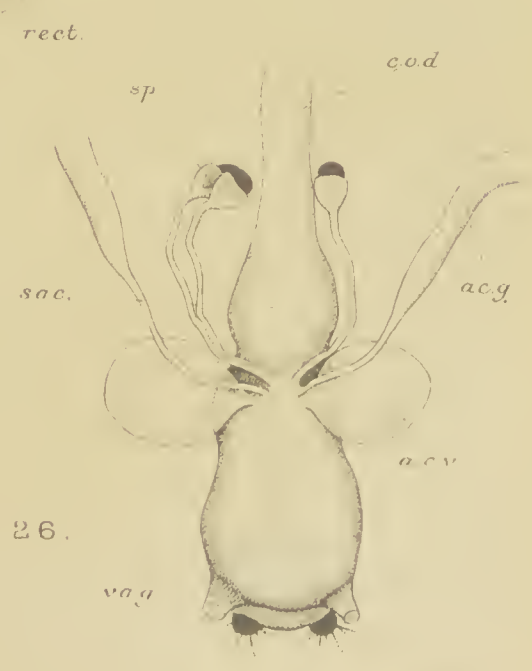
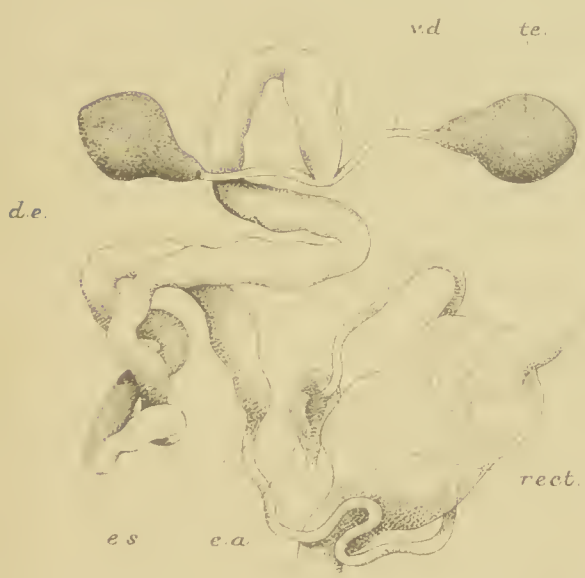
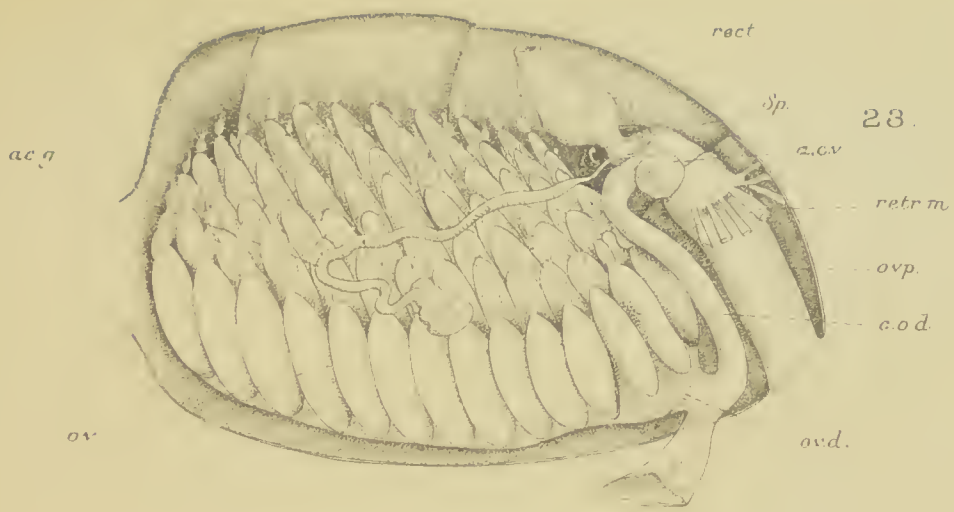
















The Structure, Development, and Bionomics of  
the House-fly, *Musca domestica*, Linn.

Part II.—The Breeding Habits, Development, and the Anatomy  
of the Larva.

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With Plates 30—33.

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## I. INTRODUCTION.

IN the present paper, which is the second of the series of three, the breeding habits and development of *M. domestica* and the anatomy of the mature larva will be described. Its publication has been delayed owing to the fact that I wished to make the observations on the breeding habits and life-history as complete as possible. With the recent appearance of two short papers by Newstead (1907) and Griffith (1908), many of whose observations, to which I shall refer later, are confirmatory of my own results, we now have a more complete account of the breeding habits of this insect.

The anatomy of the larva has been described in a similar manner to that of the fly (1907). I have refrained in this paper from giving a detailed account of the embryology and the development of the imaginal discs, as these are separate and specialised studies, and would have resulted in too great a digression from the plan originally adopted.

The methods used were the same as those previously employed. The anatomical structures were studied with the aid of the Zeiss binocular dissecting microscope, and the drawings were made from the dissections. The latter were confirmed by means of serial sections. Too much stress cannot be laid on the importance of employing both these methods where possible, as it frequently happens that mistakes are made in investigating by one method only, which would be unrectified were not the other employed in confirmation.

I wish to thank the Council of the Manchester University for providing me with a suitable experimental greenhouse and apparatus for the experimental portion of this investigation; the absence of such facilities would have been a severe handicap. The outdoor observations on the breeding habits have been made during the last few years in Manchester and the surrounding district.

The third paper, which will conclude this study of *M. domestica*, will deal with the bionomics of the fly, its para-

sites and its relation to man, and certain of its allies which frequent houses will be considered.

## II. BREEDING HABITS OF *M. DOMESTICA*.

The development of *M. domestica* was first described by Carl de Geer (1776); but, although he stated that it developed in warm and humid dung, he did not give the time occupied by the different developmental stages. He refers to the enormous quantities of flies occurring from July to August. His statement concerning their development is especially interesting, as he appears to be the first investigator who called attention to what I consider to be one of the most important factors in the development of the fly, namely, the process of fermentation occurring in the substance in which development is taking place. He says (p. 76), "*Lcs larves de cette espèce vivent donc dans le fumier, mais uniquement dans celui qui est bien chaud et humide, ou pour mieux dire qui se trouve en parfaite fermentation*" (the italics are mine). Since the completion of my own investigations on the development, all of which indicated the importance of this factor fermentation, Newstead (l. c.) has come to the same conclusion. The work of Keller (1790), to which reference was made in the first part of this memoir, contains many interesting and careful observations on the breeding habits of the "*Stubenfliege*." He found that the eggs hatched from twelve to twenty-four hours after deposition. He reared the larvæ in decaying grain where, no doubt, fermentation was taking place; also in small portions of meat, slices of melon, and in old broth. His observations are extremely interesting, and, excluding mistakes which were due to the lack of modern apparatus, his account is still a valuable contribution to our knowledge of the subject. Bouche (1834) describes the larvæ as living in horse-manure and fowl-dung, especially when warm. He does not give the time occupied by the earlier developmental stages, but states that the pupal stage lasts from 8—14 days. Packard (1874)

was the next to study the development and working in the United States of America at Salem, Mass., he found that the larvæ emerge from the eggs twenty-four hours after deposition; the times taken by the three larval stages—for he found that there were two larval ecdyses—were: first, about twenty-four hours; the second stage, he thought, was from twenty-four to thirty-six hours; and the third was probably three or four days; the entire larval life being from five to seven days. The pupal stage was from five to seven days, so that in August, when the experiments were carried on, the time from hatching to the exclusion of the imago was ten to fourteen days. Taschenberg (1880) incorporates the work of Keller and Bouche, and does not appear to add anything of importance to the facts already mentioned. He states that the female flies deposit their eggs in damp and rotting food-stuffs, bad meat, broth, slices of melon, dead animals, cesspools, and manure-heaps. He further says that they have also been observed laying their eggs in spittoons and open snuff-boxes. With reference to the last statement, I find that the larvæ will feed on expectorated matter mixed with a solid substance, such as earth, if they are kept warm, though they cannot feed on salivary sections merely; but, although flies might improvidently deposit their eggs in an open snuff-box, the larvæ would soon perish on hatching on account of the dry conditions.

Howard (1896—1906) first studied the breeding habits of the fly in 1895 in Washington, U.S.A., and he described them in 1896, and more fully subsequently. He found that they could be rarely induced to lay their eggs in anything but horse-manure and cow-dung, and that they preferred the former. The periods of development he found were as follows:—from the deposition of the egg to the hatching of the larva about eight hours; the first larval stage one day; second larval stage one day; third larval stage—that is, from the second ecdysis to pupation—three days, and the flies emerged five days after the pupation of the larvæ, thus making the whole period of development about ten days. The same

author in a valuable study of the insect fauna of human excrement (1900), describes experiments in which he was successful in rearing *M. domestica* from human excrement both in the form of loose fæces and in latrines. Newstead (l. c.), in addition to confirming some of my observations, also found the larvæ in spent hops, dirty beddings from rabbits and guinea-pigs, bedding from piggeries, and in the rotten flock beds and straw mattresses which, I suppose, were either in, or from, ashpits, and fouled with excremental products, although it is not stated. He appears to have overlooked some of the work of previous investigators.

My studies of the breeding habits of *M. domestica* were initiated in 1905, and were continued in 1906, when a short account of some of the results was published (1906). The shortest time which I then obtained for the development of any batch of larvæ was twenty days, although, taking the shortest period obtained for each developmental stage in the series of experiments, the development could have been completed in fifteen days under suitable conditions. In the summer of 1907 I continued my experiments on a much larger scale and under better circumstances, and the following are the results of my experiments and outdoor observations:

The larvæ have been successfully reared in horse-manure, cow-dung, fowl-dung, human excrement, both as isolated fæces and in ashes containing or contaminated with excrement, obtained from ashpits attached to privy middens, and such as is sometimes tipped on to public tips. I found that horse-manure is preferred by the female flies for oviposition to all other substances, and that it is in this that the great majority of larvæ are reared in nature; manure-heaps in stable yards sometimes swarm with the larvæ of *M. domestica*. It was also found that the larvæ will feed on paper and textile fabrics, such as woollen, cotton garments, and sacking which are fouled with excremental products if they are kept moist and at a suitable temperature. They were also reared on decaying vegetables thrown away as kitchen refuse, and on such fruits as bananas, apricots, cherries, plums, and peaches,



which were mixed, when in a rotting condition, with earth to make a more solid mass. Although they can be reared in such food-stuffs as bread soaked in milk and boiled egg, when these are kept at a temperature of about  $25^{\circ}$  C., I was unable to rear them to maturity in cheese, although they fed on the substances for a few days and then gradually died, my failure may have been due to the nature of the cheese which was used, only one kind being tried. In addition to rearing the larvæ on isolated human fæces, such as are frequently found in insanitary court-yards and similar places, they were found in privy middens, and also on a public tip among the warm ashes and clinker where the contents of some privy middens had also evidently been emptied; I bred the flies out from this material.

### III. FACTORS OF DEVELOPMENT.

The rate of development depends primarily on the temperature of the substance on which the larvæ are feeding. This was shown in my experiments in which the larvæ were reared in horse-manure kept in a moist condition in an incubator at a constant temperature of  $35^{\circ}$  C. At this temperature the development is completed in eight to nine days. I found that a higher temperature of  $40^{\circ}$  C. was too great for the larvæ as they were simply cooked and perished at such a temperature. This has been confirmed by Griffith (l.c.), who found that the life-history was completed in the same time on incubating at a temperature of about  $22^{\circ}$ — $23^{\circ}$  C. I do not think that a shorter time than this for the development—that is, from the deposition of the egg to the emergence of the perfect insect from the pupæ—will ever occur in this country, as we rarely enjoy prolonged spells of hot weather which would bring about such conditions as regards temperature. It is interesting to note that Smith (1907) gives the time of development in horse-manure in India under natural conditions as eight days; he also bred *M. domestica* from an artificial latrine containing human excreta mixed with earth, which confirms



English observations for India. In England, during a period of extremely hot weather, flies might develop in about nine days, but such a rate of development would not usually occur, nevertheless, as I shall show in the concluding part of this memoir, such a contingency must be guarded against. Larvæ reared in the open air in horse-manure which had an average, but not a constant, daily temperature of  $22.5^{\circ}$  C., occupied fourteen to twenty days in their development according to the air temperature.

The effect of the character of the food on which the rate of development also depends is well shown by a comparison of the times of the developmental periods in two of the experiments where the average daily temperature was practically the same, namely,  $19.3^{\circ}$  C. and  $20.5^{\circ}$  C. In the former experiment, in which human fæces were used, the development was completed in twenty days, and in the latter, in which bananas were used, the development occupied twenty-seven days; the time was rather lengthened in both cases by the fact that the larval food was rather dry, but equally dry in both experiments as they were kept together; had more moisture been present the times would probably have been correspondingly shortened.

It was experimentally proved that when larvæ were reared, in batches on the same kind of food material with conditions, as regards temperature the same, the developmental period was longer for those larvæ which were subject to dry conditions than for those subject to moist conditions. In an experiment at an average temperature of  $22^{\circ}$  C. larvæ reared on horse-manure which was kept in a rather dry condition took thirty days to complete the development, and another batch at the same temperature, but on horse manure which was kept moist, the development was completed in thirteen days. Under similar conditions, with regard to temperature, the rate of development is directly proportional to the condition of the food as regards moisture. Dry conditions not only retarded development in some of my experiments to five and six weeks, but also tended to produce flies of sub-

normal size. Moisture is necessary for the development, and if the food becomes too dry the result is fatal, as the larvæ perish.

A fourth and a most important factor affecting development and one intimately connected with the previous factors—temperature, character of food, and moisture—is that of fermentation, to which reference has already been made. This process appears to take place in the substances on which the larvæ best subsist. Whether the suitability of the food is determined by the nature of its fermentation is a point which I was unable to determine, but which I am inclined to believe. I feel certain, however, that the calorific property of fermentation is the most important part of this process on account of its direct relation to the time of development; the endogenous heat of excremental products and decaying substances acting either in addition to, or independently of, the temperature of the surrounding air is of great advantage in accelerating the rate of development.

**The Rate of Development.**—This was never found to be less than eight days, and was more usually twelve to twenty days owing to the fact that a continuously high air temperature was not maintained for any sufficient length of time; with such a continuous period of hot weather the development would take about ten to twelve days, and in very great heat might be completed in a day or two less as the internal temperature of the breeding places, such as manure-heaps is usually higher than the temperature of the air. It must be remembered, however, that except by incubation it is difficult to experimentally imitate such natural conditions as occur in a manure-heap or privy midden, where, owing to a larger amount of material, a higher constant temperature is maintained. All experimental results except those of incubation tend to give a long rather than a short rate of development. In many cases where the average temperature was 20° C., but the food material rather dry, the developmental period was about three weeks, and where the temperature was low and the food became dry it extended to

as much as six weeks, the greater time being spent in the pupal stato which was sometimes of three or four weeks duration.

In no caso was I able to keep the pupæ through the winter as I have been able to keep the pupæ of *Stomoxys calcitrans* and other forms.

My experiments and observations point to the fact that in the presenee of suitable larval food, such as excremental mattor or deeaying and fermenting food materials in a moist and warm condition, the female flies would lay their eggs and the larvæ would develop if the temperature of the air were sufficiently high for the prolonged activity of the flies. In winter this last condition is not naturally satisfied, but under such conditions as are found, for example, in warm restanrants and kitchens, stables and cowsheds, female flies may be often found during the winter. On disseeting such flies I have found mature ova in the ovaries, and living spermatozoa in the spermathecæ, which facts support this view. Griffith (l. e.) has succeeded in rearing batches of eggs in November, December, and early January under artificieal conditions, which further proves their ability, given the necessary conditions as regards temperature, to breed during the winter months. In this country *M. domestica* breeds, as a rule, from June to October, and the greatest egg-laying activity prevails in August and September. As I have already contended, and as Griffith has shown, they may breed at other times if the necessary conditions are present ; I have obtained eggs from flies caught in restaurants in December ; Keller also mentions the fact that he obtained eggs in January. These facts may account for the rapid appearance of flies in the early summer. It is not unlikely that the flies which survive the winter months, which many spend in a dormant condition if they are not fortunate enough to remain active in a warm restaurant or stable, lay their eggs, almost immediately on renowing their activity, in such places as manure-heaps which are kept, as is often the ease in towns, under cover, and which are consequently warmer externally than those in the open. In this way a large number of flies

would be reared and ready to assume their customary activity under the benign influence of the sunny days of June.

I have made many experiments with a view to finding out the rapidity with which house-flies breed. Anyone who has endeavoured to keep flies alive in an enclosed space will appreciate the difficulty of the task, those who have not done so would hardly realise it. Fewer insects seem less tenacious of life when enclosed even in a comparatively large enclosure of six or nine cubic feet. It is a remarkable fact, as one would imagine a priori that these insects, flying about everywhere as they do, could be easily kept in a roomy cage if given the necessary food and water. This, however, has not been the case in my experience; the longest period which I have been able to keep them in captivity in summer is seven weeks. I am pleased to find that Griffith has succeeded in keeping a male fly sixteen weeks, and has obtained four batches of eggs from females in captivity. In one of my experiments I was successful in obtaining flies of the second generation bred in captivity. I found that the flies became sexually mature in ten to fourteen days after their emergence from the pupal state and, four days after copulation, they began to deposit their eggs, that is, from the fourteenth day onwards from the time of their emergence.

From these results it may be seen that in very hot weather the progeny of a fly may be laying eggs in about three weeks after the eggs from which they were hatched had been deposited. As a single fly lays from 120—150 eggs at one time and may deposit five or six batches of eggs during its life, it is not difficult to account for the enormous swarms of flies that occur in certain localities during the hot summer months, and algebraical calculations are not required to more vividly impress the fact.

#### IV. DEVELOPMENT.

As I have already stated, *M. domestica* may become sexually mature in about ten to fourteen days after emer-

gence from the pupal case, and at this time they may be seen copulating.

1. The copulation of *M. domestica* appears to have been first described by Reamnr (1738). It has been carefully described recently by Berlese (1902), whose observations my own confirm. The male may perform a few tentative operations before copulation takes place, and these have been mistaken for the actual act. The male alights on the back of the female by what appears to be a carefully calculated leap from a short distance, and this act seems to indicate a faculty on the part of the fly of being able to judge distance. It then caresses the head of the female, bending down at the same time the apical portion of the abdomen. The male fly is, however, peculiarly passive during the operation, its influence apparently being only tactual, it is only when the female exerts her ovipositor and inserts it into the genital atrium of the male that copulation can successfully take place. When the ovipositor has been inserted into the genital atrium of the male, the accessory copulatory vesicles of the female become turgid and retain the terminal segment in this position, in which the female genital aperture is situated opposite to the male genital aperture at the end of the penis, the latter depending from the roof of the genital atrium. (This will be better understood by reference to the figures of these parts in Part I of this Memoir). The attachment of the penis to the female genital aperture is made still firmer by the dorsal sclerites of the eighth segment of the female and the ventral sclerites of the seventh segment, the so-called secondary forceps of the male acting respectively above and below the penis. The fifth ventral segment, or primary forceps of the male, assist the accessory copulatory vesicles of the female in preventing the withdrawal of the ovipositor before the spermatozoa have been injected into the female genital aperture, by which way they enter the spermathecae. The whole act may be over in a few moments or they may remain in coitu for several minutes.

The eggs are laid a few days after copulation; I found



that oviposition may take place as early as the fourth day; Taschenberg (t. c.) states that the female lays on the eighth day after copulation. When about to deposit its eggs the fly alights on the substance which it selects as a suitable nidus and, if possible, crawls down a crevice out of sight. There it lays its eggs in clumps; they are usually placed vertically on their posterior ends and closely packed together. During a single day, if undisturbed, a fly may lay the whole batch of eggs which are mature in the ovaries and which may number, I find from actual count, from 120—150.

2. The Egg.—The egg of *M. domestica* (Pl. 30, fig. 1) measures 1 mm. in length, sometimes slightly less. It is cylindrically oval; one end, the posterior, is broader than the other, towards which end the egg tapers off slightly. The outer covering or chorion is pearly white in colour, the polished surface being very finely sculptured with minute hexagonal markings. Along the dorsal side of the egg are two distinct curved rib-like thickenings having their concave faces opposite. In the hatching of the eggs which I have observed, the process was as follows:—A minute split appeared at the anterior end of the dorsal side to the outside of one of the ribs; this split was continued posteriorly (fig. 2), and the larva crawled out, the walls of the chorion collapsing after its emergence. The time of hatching varies according to the temperature. With a temperature of 25°C.—35°C. the larvæ hatch out from eight to twelve hours after the deposition of the eggs; at a temperature of 15°C.—20°C. it takes about twenty-four hours, and if kept as low as 10°C., two or three days elapse before the larvæ emerge.

3. The Larva.—First larval stage or first instar.—The newly-hatched larva (fig. 8), measures 2 mm. in length. It contains the same number of segments as the mature larva and at the anterior end of the ventral surface of each of the posterior eight segments there is a spiny area (*sp.*). The posterior end is obliquely truncate, and bears centrally the only openings of the two longitudinal tracheal trunks, each trunk opening to the exterior by a pair of small oblique slit-



like apertures situated on a small prominence (*p.sp.*). There are no anterior spiracular processes in the first larval stage. The oval lobes are relatively large and on the internal ventral surface of each there is a small T-shaped sclerite (fig. 13, *t.s.*). These sclerites lie lateral to the falciform mandibular sclerite (*m.s.*). The cephalopharyngeal skeleton of the first larval instar is slender and, in addition to the sclerites already mentioned, consists of a pair of lateral pharyngeal sclerites or plates (*l.p.*) deeply incised posteriorly, forming well pronounced dorsal and ventral processes. The lateral plates are connected antero-dorsally by a curved dorsal sclerite (*d.p.s.*). The anterior edges of the lateral plates are produced ventrally into a pair of slender processes (*h.s.*), the anterior portions of these processes, which represent the hypostomal sclerite, are involute and articulate with the mandibular sclerite. The alimentary canal of the first larval instar is relatively shorter than that of the adult, and consequently it is not so convoluted; the salivary glands are proportionately large.

The first larval instar may undergo ecdysis as early as twenty hours after hatching, but it is usually from twenty-four to thirty-six hours that the ecdysis takes place: under unfavourable conditions with regard to the factors governing the development, the first larval instar sometimes lasted three or four days. Ecdysis begins anteriorly, and the larva not only loses its skin but also the cephalopharyngeal sclerites which are attached to the stomodæal portion of the ecdysed chitinous integument; the chitinous lining of the proctodæal portion of the alimentary tract is also shed.

The second larval stage or second instar. This stage is provided with a pair of anterior fan-shaped spiracular processes similar to those of the mature larva. The posterior spiracular orifices are shown in fig. 12. They are slit-like apertures rather similar to those of the first instar but larger in size. The cephalopharyngeal skeleton is thickened and less slender in form than that of the first instar. It resembles the cephalopharyngeal skeleton of the mature larva except that the posterior sinuses of the lateral pharyngeal

sclerites are much deeper, thus making the dorsal and ventral posterior processes more slender than in the mature larva. The second larval instar may undergo ecdysis in twenty-four hours at a temperature of 25°—35°C., but under cooler conditions or with a deficiency of moisture the period is prolonged and may take several days.

The third larval stage or third instar, which is the last larval stage, grows rapidly. The anatomy of this the mature larva will be fully described. Larvæ incubated at a temperature of 35°C. complete this larval stage and pupate in three to four days, on the other hand, under less favourable developmental conditions, it sometimes extended over a period of eight or nine days. Incubated larvæ cease feeding at the end of the second day of this stage and gradually assume a creamy colour, which colour is due to the large development of the fat body and to the histolytic changes which are taking place internally; larvæ dissected at this stage contain a very large amount of adipose tissue cells. Between the third and fourth day the larva contracts to form the pupa.

4. The Pupa.—The process of pupation may be completed in so short a time as six hours. The larva contracts, the anterior end especially being drawn in, with the result that a cylindrical pupal case is formed (fig. 15), the posterior region being very slightly larger in diameter than the anterior; the anterior and posterior extremities are evenly rounded. The average length of the pupa is 6.3 mm. Owing to the withdrawal of the anterior segments the anterior spiracular processes (*a.sp.*) are now situated at the anterior end, and the posterior spiracles (*p.sp.*) form two flat button-like prominences on the posterior end. The pupa changes from the creamy-yellow colour of the larva to a rich dark brown in a few hours. As the last larval skin has formed the pupal case, it being a coarctate pupa, in addition to the persistence of the spiracular processes the other larval features such as spiny locomotory pads can be seen.

During the first twelve hours or so of pupation the larva loses its tracheal system, which appears to be withdrawn

anteriorly and posteriorly, the latter moiety being the larger; the discarded larval tracheal system lies compressed against the interior of the pupal case (*l.tr.*). Communication with the external air is formed for the nymphal<sup>1</sup> developing tracheal system by means of a pair of temporary pupal spiracles, which appear as minute spine-like lateral projections between the fifth and sixth segments of the pupal case (*n.sp.*). Each of these communicates with a knob-like spiracular process (fig. 10, *n.sp.*) attached to the future prothoracic spiracle of the fly. The proctodæal and stomodæal portions of the alimentary tract are also withdrawn, and with the latter the cephalo-pharyngeal skeleton, which lies on its side on the ventral side of the anterior end of the pupal case.

The histogenesis of the nymph is extremely rapid, so that at the end of about thirty hours, in the rapidly developing specimens, it has reached the stage of development shown in fig. 10, in which most of the parts of the future fly can be distinguished although they are ensheathed in a protecting nymphal membrane. The head, which with the thorax has been formed by the eversion of the cephalic and thoracic imaginal discs from their sacs, is relatively large: two small tubercles (*an.*) mark the bases of the antennæ. The proboscis is enclosed in a large flat sheath which at this period appears to be distinctly divided into labral (*lbr.*) and labial (*lb.*) portions. In a short time the parts of the proboscis are seen to develop in these sheaths (fig. 11). The femoral and tibial segments of the legs are closely adpressed and lie within a single sheath. The wings (*w*) appear as sac-like appendages, and, as the nymphal sheath of the wing does not grow beyond a certain size, the wing develops in a slightly convoluted fashion by means of a fold which appears in the costal margin a short distance from the apex of the wing.

With a constant temperature of about 35° C., or even less, the exclusion of the imago may take place between the third

<sup>1</sup> The word "nymph" is used here to designate that stage in the development which begins with the appearance of the form of the future fly, and ends when the exclusion of the imago takes place.

and fourth day after pupation, but it is more usually four or five days as the larvæ, when about to pupate, leave the hotter central portion of the mass in which they have been feeding and pupate in the outer cooler portions: this outward migration may be a provision for the more easy emergence of the excluded fly from the larval nidus. In some cases the pupal stage lasts several weeks, but I have never succeeded in keeping pupæ through the winter.

When about to emerge, the fly pushes off the anterior end of the pupal case in dorsal and ventral portions by means of the inflated frontal sac, which may be seen extruded in front of the head above the bases of the antennæ. The splitting of the anterior end of the pupal case is quite regular, a circular split is formed in the sixth segment and two lateral splits are formed in a line below the remains of the anterior spiracular processes of the larva. The fly levers itself up out of the barrel-like pupa and leaves the nymphal sheath. With the help of the frontal sac which it alternately inflates and deflates it makes its way to the exterior of the heap and crawls about while its wings unfold and attain their ultimate texture, the chitinous exoskeleton hardening at the same time; when these processes are complete the perfect insect sets out on its career.

## V. THE LARVA OF MUSCA DOMESTICA.

1. External Features.—The external appearance of the typical acephalous muscid larva or "maggot" (fig. 5) is well known. It is conically cylindrical. The body tapers off gradually to the anterior end from the middle region. The posterior moiety is cylindrical, and except for the terminal posterior segment the segments are almost equal in diameter. The posterior end is obliquely truncate. The enticular integument is divided by a number of rings; this ringed condition is brought about by the insertion of the segmentally-arranged somatic muscles the serial repetition of which can

be clearly understood by reference to fig. 16. The average length of the full-grown larva of *M. domestica* is 12 mm.

The question as to the number of segments which constitute the body of the muscid larva is a debated subject. I have, however, taken as my criterion the arrangement of the somatic musculature. Newport (1839) considered that the body of the larva of *Musca vomitoria* consisted of fourteen segments, but if the anterior portion of the third segment, that is, my first post-oral segment, is included, there were fifteen, to which view he appeared to be inclined. Counting the anterior segment or "head" as the first, Weismann (1863 and 1864) considers that the body is composed of twelve segments. Brauer (1883) is of the opinion that there are twelve segments, but that the last segment is made up of two; Lowne follows this view in his description of the blow-fly larva and considers that there are fifteen post-oral segments. I am unable to accept Lowne's view. Counting the problematical cephalic segment, for which I shall use Henneguy's (1904) term "pseudo-cephalon," as the first segment, I believe that it is succeeded by twelve post-oral segments, making thirteen body segments in all, which is the usual number for dipterous larvæ as Schiner (1862) has also pointed out. My study of the somatic musculature, as I shall show, indicates the duplicate nature of the apparent first post-oral segment, so that the apparent second post-oral segment (iv), that is, the segment posterior to the anterior spiracular processes, is really the third post-oral segment or fourth body-segment.

The cephalic segment cannot be considered as homologous with the remaining twelve segments, which are true segments of the body as shown by their musculature and innervation. This segment (fig. 9, i), for which Henneguy's term "pseudo-cephalon" is very suitable, probably represents a much reduced and degenerate cephalic segment, its present form being best suited to the animal's mode of life. We may consider the greater part of the cephalic segment of the larva as having been permanently retracted within the head; this is shown by



the position of the pharyngeal skeleton, to the whole of which the name "cephalo-pharyngeal skeleton" has been given. All that now is left of the cephalic segment consists of a pair of oral lobes, whose homology with the maxillæ is very problematical, and at present is not safely tenable. On the dorsal side the oral lobes are united posteriorly. Each bears two conical sensory tubercles (*o. t.*), which are situated, the one dorsally, and the other anterior to this and almost at the apex of the oral lobe. The ventral and ventro-lateral surfaces of the oral lobes are traversed by a number of channels, which will be described later.

The post-cephalic segment, which is composed of the first and second post-oral segments and represents the second and third segments of the body, is conical in shape. The first post-oral segment (ii), to which Lowne gave the name "Newport's segment," is limited posteriorly by a definite constriction and is covered with minute spines. The second post-oral segment bears laterally at its posterior border the anterior spiracular processes (*a. sp.*) The remaining segments of the body—four to twelve—are on the whole similar in shape. At the anterior edge of the ventral side of each of the sixth to twelfth body-segments there is a crescentic pad (fig. 5, *sp.*) bearing minute and recurved spines; these are locomotory pads by means of which the larva moves forwards and backwards. It is important to note that these pads are situated on the anterior border of the ventral side of each segment as they do not appear to have been carefully placed in the previous figures of this species. In addition to these spiniferous pads there are two additional pads of a similar nature, one on the posterior border of the ventral side of the twelfth body-segment, and the other posterior to the anus.

The terminal or thirteenth body-segment is obliquely truncate, but the truncate surface, which occupies more than half the posterior end of the larva, is not very concave as in the blow-fly larva. It bears in the centre the two posterior spiracles (fig. 3, *p. sp.*), which are described in detail with the tracheal system. On the ventral side of the terminal segment



are two prominent anal lobes (fig. 5, *an. l.*), which are important agents in locomotion.

The cuticular integument is thin and rather transparent, so that in the younger larvæ many of the internal organs can be seen through it. In older larvæ the fat-body assumes large proportions and gives the larva a creamy appearance, obscuring the internal organs. The cuticle (fig. 14) is composed of an outer rather thin layer of chitin (*ct.*), which is continuous with the chitinous intima of the tracheæ, and also with the chitinous lining of the stomodæal and proctodæal regions of the alimentary tract. Below this layer there is a thicker layer of chitin (*ct.'*), which does not stain so deeply. In places this lower layer is penetrated by the insertions of the muscles. The cuticle lies on a layer of stellate hypodermal cells (*hy.*), which are well innervated, and attain a large size in the posterior segments of the body.

## 2. MUSCULAR SYSTEM.

The muscular system of the larva (Pl. 31, fig. 16) consists of a segmental series of regularly repeated cutaneous muscles, forming an almost continuous sheath beneath the skin, together with a set of muscles in the anterior segments of the body which control the cephalo-pharyngeal sclerites and pharynx. In addition to this there are a set of cardiac muscles and the muscles of the alimentary tract.

I have been unable to find a detailed description of the muscular system of the muscid larva, and I do not think that Lowne's excuse for dismissing the cutaneous muscles of the blow-fly larva with a very brief statement, because "the details possess little or no interest," was justified, considering how little is known about the muscular systems of insect larvæ, and constant reference to the classic work of Lyonet (1762) on the caterpillar is not sufficient to satisfy the inquiring student of to-day. The muscular system of the larva, therefore, will be described in some detail.

Muscles of the body-wall.—The cutaneous muscles

are repeated fairly regularly from segments (by segments I mean body-segments) four to twelve and a detailed description of the muscles of one of these segments will serve for the rest. The muscles, though continuous in most cases from segment to segment, are attached to the body-wall at the junction of the segments. The most prominent muscles are the dorso-lateral oblique recti muscles. In segments six to twelve there are four pairs each of external (*ex. d. l.*), and internal dorso-lateral oblique recti (*in. d. l.*) muscles; in segments four and five there are five pairs of external and six pairs of internal dorso-lateral oblique muscles. Ventral to these muscles are four pairs of longitudinal ventro-lateral muscles (*l. v. l.*); the muscle bands of the two more ventral pairs are double the width of those of the two more lateral pairs. In the fifth segment there is only one of the more lateral pairs of the longitudinal ventro-lateral muscles present, and in the fourth segment only the two more ventral pairs remain. In addition to these muscles there are two other pairs of oblique recti muscles; these are, a pair of ventro-lateral oblique muscles (*v. l. o.*) and a pair of internal lateral oblique muscles (*i. l. o.*); both of these are absent in the segments anterior to the sixth. The foregoing muscles, namely the dorso-lateral oblique, the internal lateral oblique, the ventro-lateral oblique and the longitudinal ventro-lateral, by their contraction, bring together the intersegmental rings and so contract the body of the larva.

Attached externally to the anterior ends of the longitudinal ventro-lateral muscles are a number of pairs of ventral oblique muscles (*v. o.*); they vary in number from two to eight pairs in each segment. The number increases posteriorly from two pairs in segment four to four pairs in segment five, five pairs in segment seven, seven pairs in segment ten, eight pairs in segment eleven; the number of pairs then decreases to six or seven pairs in segment twelve. The more ventral pairs of these muscles are not attached at their posterior ends to the intersegmental ring but to the ventral wall of the segment and no doubt assist in bringing forward the ventral spiniferous pads. In segments four to twelve there are three pairs of

lateral muscles (*l. m.*) situated next to the hypodermis and attached in a dorso-ventral position; these will assist in drawing the dorsal and ventral regions of the segments together and so increase the length of the larva. Between segments four and five and the remaining segments to twelve there is, on the intersegmental ring, a pair of lateral intersegmental muscles (*l. i. m.*); these by their contraction bring about a decrease in the size of the intersegmental ring and so assist the lateral muscles in increasing the length of the larva.

The muscles of the last segment (xiii) are not regularly arranged as in the preceding segments; they consist of three main groups: (1) the recti muscles, which assist in contracting the segments; (2) the anal muscles (*an. m.*), which are attached ventrally to the anal lobes (*an. l.*); and (3) the dorso-ventral muscles (*d. v.*), which by their contraction assist in lengthening the segment. In addition to these there are certain small muscles in relation with the posterior spiracles.

In the second and third segments the recti muscles are reduced to four pairs and the attachment of the two lateral and external pairs of muscles has led me to regard the apparently single first post-oral segment as consisting of two segments; it is not a single post-cephalic or pro-thoracic segment as it has been called. There is quite a distinct internal division and the external constriction has been already noticed. This view does not necessarily alter the homology of the third segment, which may still be regarded as pro-thoracic if this is desirable. The segment which I regard as the second body-segment may be a rudiment of the cephalic region which has been almost lost, and this loss, or, as I prefer to regard it, this withdrawal of the head, only serves to make any discussion as to the homologies of these anterior segments with those of the adult extremely difficult, and, I believe, at present valueless. Further, comparative studies of the larvæ of the ealyptrato muscidæ are necessary before we can arrive at any definite conclusions concerning the composition of the bodies of these larval forms.

The cephalo-pharyngeal muscles (fig. 19).—These muscles consist of four sets: (1) The cephalic retractor muscles, which by their contraction draw the anterior end of the larva and the pharyngeal mass inwards; (2) the protractor and depressor muscles of the pharyngeal mass; (3) the muscles controlling the mandibular, dentate, and hypostomal sclerites; and (4) the internal pharyngeal muscles.

There are four chief pairs of cephalic retractor muscles, of which the two ventral pairs are by far the largest. The more ventral of these two pairs (*v'. c. r.*) arises on the ventral side from the posterior end of the sixth segment, internal to the ventro-lateral longitudinal muscles; the other pair (*v. c. r.*), which is double, arises more laterally from the posterior end of the fifth segment. The remaining pairs of cephalic retractors arise from the posterior end of the third segment. All the cephalic retractor muscles are inserted anteriorly into a ring, the cephalic ring (*c. r.*), on the anterior border of the second segment, the first post-oral segment.

There are two pairs of cephalo-pharyngeal protractor muscles, a dorsal (*d. c. p.*) and a ventral pair (*v. c. p.*). Both are rather broad fan-shaped muscles inserted by their broad ends in the middle of the third segment, slightly to the sides of the dorsal and ventral median lines respectively. The dorsal and ventral muscles of each side are inserted together on the dorso-lateral region of the posterior end of the pharyngeal mass. The pair of depressor muscles (*d. m.*) which are situated dorsally, are attached by their broader ends to the intersegmental ring between segments three and four. They are inserted on to the posterior end of the dorsal side of the pharyngeal mass; by their contraction the posterior end of the pharyngeal mass is raised, the result being that the sclerites articulated to its anterior end are depressed.

There remain six pairs of muscles controlling the mandibular, dentate and hypostomal sclerites, one pair controlling the two foremost sclerites and four pairs controlling the hypostomal sclerite. The mandibular extensor muscles (*m. e.*) are attached to the body-wall in the third segment on each side

of the median line and between the dorsal eephalo-pharyngeal protraectors. They are inserted on to the dorsal side of the mandibular selerite (*m. s.*); by their contraction they elevate the selerite. This selerite is depressed by the contraction of a pair of muscles which control the dentate selerites (*d. s.*), the latter fitting into a notch on the ventral side of the mandibular selerite. The mandibular depressor muscle (*m. d.*) is attached to the posterior ventral process of the lateral pharyngeal selerite by the three bands into which the posterior portion of the muscle is divided; the anterior and single end of the muscle is inserted on the ventral process of the dentate selerite. Four pairs of muscles (*s. d.*) are inserted on the hypostomal selerite (*h. s.*). Two more dorsal pairs are attached to the intersegmental ring between segments three and four as shown in fig. 16. The two more ventral pairs are attached to the lateral pharyngeal sclerites, one being attached to the ventral side of the posterior dorsal process and the other to the ventral process beneath the mandibular depressor. These muscles, which I call the stomal dilators, are inserted on the sides of the hypostomal selerite. Their function is, I believe, to open and close the anterior pharyngeal aperture and so control the flow of fluid food into the pharynx and of the salivary secretion; the lowest pair of muscles may be more directly concerned with the latter.

The pharyngeal apparatus is controlled, as in the adult fly, by a series of muscles. In the larval stadium, however, where so large an amount of food is required for the growth and building up of the future insect, there is a greater development and elaboration of the pharyngeal apparatus, including the muscles. In the greater anterior region of the pharynx, that is, the part lying within the pharyngeal sclerites (fig. 18), the muscular system consists of two bands of oblique muscles (*o. ph.*) arranged in pairs. The muscles are attached dorsally to the inside dorsal edges of the lateral plates (*l. p.*) and ventrally to the roof of the pharynx (*r. ph.*), the ventral attachment being more posterior than the dorsal. The posterior region of the pharynx, which is between the lateral plates and



the œsophagus (fig. 17), is controlled by two sets of muscles. Two pairs of elongate oblique muscles (*e. o. m.*) are attached dorsally to the dorsal edges of the lateral plates (*l. p.*) and inserted ventrally on to the roof of the pharynx; these muscles assist the previously described oblique pharyngeal muscles in raising and depressing the roof of the pharynx. They are assisted in enlarging and contracting the lumen of the posterior part of the pharynx by a number of semi-circular dorsal muscles (*s. d. m.*), which by their contraction make the floor of the pharynx more concave, and it is these muscles, I believe, that are chiefly concerned in the maintenance of the peristaltic contractions of the pharynx, by means of which the fluid food, which has been sucked into the mouth by the pumping action of the pharynx, is carried on to the œsophagus.

The similarity between the pharyngeal apparatus of the fly, that is, of the fulcrum and that of the larva, is very striking, both with regard to the form of the skeletal structures and the musculature. If the pharynx of the larva were regarded as being homologous to that of the fly it would further support the view that the head of the larva had been permanently withdrawn into the succeeding anterior body-segments. These structures, however, may be merely analogous; the similarity of structure may have been brought about by similarity of function. Both larva and adult subsist on fluids which are sucked into the mouth and pumped into the œsophagus.

The series of muscular actions which takes place during locomotion appears to be as follows. By the contraction of the pharyngeal protractors the anterior end of the larva is extended, the mandibular sclerite being extended at the same time by the contraction of the mandibular extensor muscles. The mandibular sclerite is now depressed by the contraction of the mandibular depressors, and anchors the anterior end of the larva to the substance through which it is moving. A series of segmental linear contractions now takes place, initiated by the large cephalic retractor muscles, and carried on posteriorly from segment to segment by the



dorso-lateral oblique, the internal lateral oblique, the longitudinal ventro-lateral, the ventro-lateral oblique and ventral oblique muscles. Each segment as it comes forward takes a firm grip ventrally by means of the spiniferous pad. By the time the last spiniferous pad has become stationary the mandibular selerite has left its anchorage, and by the contraction of the lateral and intersegmental muscles, which takes place from before backwards, the lengths of the segments of the larva are increased serially and the anterior end begins to move forward again, when the whole process is repeated.

### 3. NERVOUS SYSTEM.

The central nervous system of the larva (Pl. 32, fig. 23) has attained what would appear to be the limit of ganglionic concentration and fusion. The boat-shaped ganglionic mass, which lies partly in the fifth segment, but the greater portion in the sixth segment, is a compound ganglion and represents the fusion of eleven pairs of ganglia similar to that which Leuckart (1858) describes in the first larval stage of *Melophagus ovinus*, but which, however, has not undergone so great a degree of concentration as in *M. domestica*. This ganglionic mass, which for convenience and brevity I shall call the ganglion (Lowne's "neuroblast") does not exhibit externally any signs of segmentation, the interstices between the component ganglia being filled up with the cortical tissue, whose outer wall forms a plain surface. In horizontal and sagittal sections, however, the component ganglia can be recognised and their limits are more clearly defined. The ganglion is surrounded by a thick ganglionic capsular sheath which is richly supplied with tracheæ, and appears to be continuous with the outer sheath of the peripheral nerves. Two pairs of large tracheæ (fig. 24) are found entering the ganglionic sheath, an anterior pair (*tr.* ') which runs in between the cerebral lobes, and a lateral pair (*tr.* ") entering the ganglion beneath these lobes. In the young larva the cortical

layer of cells is proportionately much thicker. The cortical tissue is made up of cells of varying sizes, but which can be grouped in two classes—smaller cortical cells and larger ganglionic cells. Most of the ganglionic cells appear to be unipolar, but there are many of a bipolar and multipolar nature present; they stain readily and possess fairly large nuclei. These ganglionic cells are arranged segmentally, and occur near the origin of the nerves. In the posterior region of the ganglion, where the nerves arise in close proximity, the ganglion cells are very numerous, relatively few of the cortical cells being found. A further demarcation of the component ganglia is brought about by median and vertical strands of the ganglionic sheath-tissue, which perforate the compound ganglion and occur as vertical strands along its median line. Tracheæ also penetrate the ganglion with these strands of capsular tissue.

On the dorsal side of the anterior end of the ganglion is situated a pair of spherical structures (*c. l.*), which may be termed the “cerebral lobes.” They are united in the median line dorsal to the foramen traversed by the œsophagus (*œ.*). These cerebral lobes are chiefly of an imaginal character, and contain the fundamentals of the supra-œsophageal ganglia and also of the optic ganglia of the future fly (fig. 27). Each is surrounded by a thin membranous sheath (*sh.*) and is connected with the major cephalic imaginal discs by the optic stalk (*o. s.*).

The nerves arising from the ganglion may be divided into three groups, according to their origin. Eleven pairs of nerves (fig. 24, 1–11) corresponding to the eleven pairs of ganglia arise, two from the anterior end and nine from the sides of the ganglion. Three pairs of nerves (*a.*, *b.* and *c.*) arise laterally from the stalks of the pro-thoracic and meso-thoracic imaginal discs. In the median dorsal line of the posterior half of the ganglion a single pair (*d. a.*′) and two median unpaired (*d. a.*″ *d. a.*″′) nerves have their origin; these are accessory nerves.

The first pair of the two anterior pairs of nerves runs

forward and innervates the posterior region of the pharyngeal mass; the anterior region of the latter is supplied by the second pair of nerves. These nerves also innervate the anterior segments of the body. The first (*a*) of the three pairs of nerves which arise from the stalks of the imaginal discs runs to the anterior end supplying the protractor and retractor muscles of the pharyngeal mass. The second (*b*) of these three pairs of nerves innervates the muscles of the body-wall of the third and fourth segments; the latter segment is also innervated by the third (*c*) of the three pairs of nerves. The succeeding nine pairs of lateral nerves are segmentally distributed, and innervate the muscles of the body-wall of segments five to thirteen. Each nerve bifurcates on reaching the muscles, and these branches further subdivide into very fine nerves.

The nerves, which arise dorsally, and which I have called the accessory nerves, are interesting. The first pair (*d. a.*') which arises about mid-way along the dorsal side of the ganglion, accompanies the pair of nerves supplying the seventh segment. The second (*d. a.*'), which is an unpaired nerve, bifurcates in the seventh segment, and the resulting nerves proceed to the body-wall in association with the nerves supplying the eighth segment. The third and posterior dorsal accessory nerve (*d. a.*''') bifurcates in the seventh segment. Each of the resulting nerves undergoes a second bifurcation; the dextral nerve, bifurcating in the eighth segment, accompanies the nerves supplying the ninth segment; the sinistral nerve bifurcates between segments eight and nine, and the resulting nerves proceed to the tenth segment. None of the remaining lateral nerves appear to be accompanied by an accessory nerve, of which there are four pairs only. The ganglionic sheath is penetrated by tracheæ, some of which arise from the ganglion in association with the nerves which they accompany to the body-wall. Two of these tracheæ are shown (fig. 24, *t.*). Similar fine tracheæ arise with the three posterior pairs of lateral nerves, and on account of their similarity to accessory nerves I at first

mistook them for such, even when dissecting with a magnification of sixty-five diameters, until my serial sections showed their real nature. Without sections it is impossible to distinguish these fine unbranching tracheæ from accessory nerves. I have mentioned this fact as showing the necessity of supplementing the one method by the other.

The visceral or stomatogastric nervous system (Pl. 31, fig. 20) consists of a small central ganglion (*c. g.*) lying on the dorsal side of the œsophagus, immediately behind the transverse commissure of the cerebral lobes from the bases of which two fine nerves are given off to join a fine nerve from the ganglion, which runs dorsally towards the anterior end of the dorsal vessel. A fine nerve from the ganglion runs forward on the dorsal side of the œsophagus towards the pharynx. A posterior nerve (fig. 24, *v. n.*) runs from the ganglion along the dorsal side of the œsophagus to the neck of the proventriculus, where it forms a small posterior ganglion (fig. 20, *pv. g.*), from which fine nerve-fibres arise and run over the anterior end of the proventriculus.

Sensory organs.—The only sensory organs which the larva possesses are the two pairs of conical tubercles (fig. 9, *o. t.*), which have been described already on the oral lobes. In section each consists of an external transparent sheath of the outer cuticular layer; beneath this and surrounded by a chitinous ring are the distal cuticularised extremities of a number of elongate fusiform cells grouped together to form a bulb. These are nerve-end cells and their proximal extremities are continuous with nerve-fibres by means of which they are connected to the ganglion. Both sensory organs of each oral lobe are supplied by the same nerve from the second of the two anterior nerves. Judging from their structure these organs appear to be of an optical nature, and this is the usual view which is held with regard to their function. They would appear merely to distinguish light and darkness, which, for such cryptophagous larva, is no doubt all that is necessary. The negative heliotropism of the larva of the blow-fly has been experimentally proved by Loeb (1890), and my own

observations confirm the same for the larvæ of *M. domestica*.

The hypodermal cells are well innervated and the body-wall appears to be highly sensitive.

#### 4. THE ALIMENTARY SYSTEM.

The alimentary tract increases in length at each of the larval ecdyses, and in the mature larva (Pl. 33, fig. 29), its length is several times greater than the length of the larva. The great length of the alimentary tract of the larva compared with that of the fly is probably accounted for by the fact that a large digestive area is necessary for the rapid building up of the tissues from fluid food which takes place during the larval life. It is divisible into the same regions as the alimentary tract of the mature insect, but it differs from the latter in several respects; these regions are parts of the original stomodæal, mesenteric and proctodæal regions of which the mesenteric is by far the longest in this larva. The regions of the alimentary tract which are derived from the stomodæum and proctodæum are lined with chitin of varying thickness which is attached during life to the epithelial cells, but is shed when the larva undergoes ecdysis. The mesenteron does not appear to be lined with chitin as it is in some insects, in which cases the chitinous intima usually lies loose in the lumen; it is, however, in the larva of *M. domestica*, usually lined with a lining of a mucous character. The whole alimentary tract is covered by a muscular sheath of varying thickness.

The mouth (fig. 6, *m.*) opens on the ventral side between the oral lobes. The ventral and ventro-lateral sides of the oral lobes are traversed by a series of small channels (fig. 14, *ch.*), which are made more effective by the fact that one side of the channel is raised and overhangs the other so as to partially convert the channels into tubes rather comparable to the pseudo-tracheæ of the oral lobes of the fly, to which they have a similar function: the liquid food runs along these



channels to the mouth. Distally many of the channels unite; the resulting channels all converge and run into the mouth. The anterior border of the oral aperture is occupied by the mandibular sclerite (*m. s.*), and the posterior border is bounded by a lingual-like process (*l.*) that is bilobed at its anterior extremity.

Cephalo-pharyngeal sclerites (Pl. 30, fig. 4).—The sclerites associated with the cephalo-pharyngeal region are rather similar to those of the second larval instar; they are, however, of a more solid and of a thicker character. Between the oral lobes is seen the median uncinat mandibular sclerite (*m. s.*). The homology of this sclerite is obscure. Lowne regarded it as being the labrum; some authors consider that it represents the fused mandibles. As we know at present so little of the comparative embryology of these larvæ it will be best to retain the name by which it is generally known. The basal extremity of the mandibular sclerite is broad, and at each side a dentate sclerite (*d. s.*) is articulated by means of a notch in the side of the mandibular sclerite, the function of which has been shown already in describing the muscles. The mandibular sclerite articulates posteriorly with the hypostomal sclerite (*h. s.*). This consists of two irregularly-shaped lateral portions united by a ventral bar of chitin; it is anterior to this bar of chitin that the salivary duct opens into the front of the pharynx. The sides of the hypostomal sclerite articulate with two processes on the anterior edge of the lateral pharyngeal sclerites (*l. p.*). The lateral pharyngeal sclerites or plates recall the shape of the fulcrum of the adult fly. Each is wider posteriorly than anteriorly, and the posterior end is deeply incised; at the base of this incision the nerves and tracheæ which supply the interior of the pharynx enter. The lateral sclerites vary in thickness, as will be seen in the figures of the sections of the pharynx. They are united dorsally at the anterior end by a dorsal sclerite (*d. p. s.*), and ventrally they are continuous with the floor of the pharynx.

The pharynx (Pl. 31, figs. 17 and 18) in certain respects is



similar to that portion of the pharynx of the fly which lies in the fulcrum. The whole length of the floor of the pharynx is traversed by a series of eight grooves separated by bifurcating ribs which are T-shaped in section (fig. 18, *t. r.*), and are called the "T ribs" by Holmgren (1904); they form a series of eight tubular grooves. Holmgren believes that they may have been derived from a condition similar to that found in the pharynx of the larva of *Phalacroceras*, where the floor of the pharynx is traversed by a number of deep but closed longitudinal fissures. These pharyngeal grooves probably have a straining function, but they may also be of use in allowing a certain amount of the salivary secretion to flow backwards towards the œsophagus. The musculature and action of the pharynx has been described. On the dorsal side of the pharyngeal mass and attached laterally to the layer of cells covering the lateral sclerites there is a loose membrane (*m.*), whose function, I believe, is to accommodate the blood contained in the pharyngeal sinus (*p.s.*) when the roof of the pharynx is raised. Posteriorly the floor of the pharynx curves dorsally and opens into the œsophagus.

The œsophagus (fig. 29, *œ.*) is a muscular tube beginning at the posterior end of the pharyngeal mass. It describes a dorsal curve when the larva is contracted, and then runs in a straight line through the œsophageal foramen between the cerebral lobes of the ganglionic mass and dorsal to the ganglion to the posterior region of the sixth larval segment, where it terminates and opens into the proventriculus. It is of a uniform width throughout and is lined by a layer of flat epithelial cells (fig. 25, *œ. ep.*) whose internal faces are lined by a chitinous sheath (*ch. i.*), which is thrown into a number of folds. There is nothing of the nature of a ventral diverticulum forming a crop such as Lowne describes in the larva of the blow-fly.

The proventriculus (fig. 29, *pv.*) varies slightly in shape according to the state of contraction of the alimentary tract; in the normal condition it is cylindrically ovoid and its axis is parallel with that of the body. As will be seen from the

figure (fig. 25), it is rather similar to the proventriculus of the imago in general structure. The œsophageal epithelium penetrates a central core which is composed of large clear cells (*c. c.*); its lumen, being œsophageal, is lined with chitin. This core is surrounded by an outer sheath, the cells (*e. v.*) of which are continuous with those of the ventriculus. At the junction of the central core with the outer sheath of cells there is a ring of small more deeply-staining cells (*i. c.*). This ring was regarded by Kowalevski (1887) as the rudiment of the stomodæum of the nymph, but Lowne is of the opinion that it develops in the nymph into the proventriculus of the imago. I believe that it forms a portion, at least, of the proventriculus of the imago, as it exhibits a very close resemblance to the ring of cells in this region figured in the section of the proventriculus of the imago (fig. 20 of Part I).

The mesenteron of the mature larva is of very great length, and is not divisible into the two regions of ventriculus and small proximal intestine as in the imago, but appears to have the same character throughout; hence Lowne calls it the "chyle-stomach," which term, or ventriculus (fig. 29, *v.*), may be used to designate the whole region from the proventriculus to the point at which the malpighian tubes arise. It is very much convoluted and twisted upon itself. The course of the ventriculus is almost constant, and can be better understood from the figure than from any detailed description. At the anterior end four tubular cæca (*c. v.*) arise. Their walls consist of large cells whose inner faces project into the lumen of the glands; these glands were not present in the imago. The epithelium of the ventriculus (fig. 30) is composed of large cells (*e. v.*), which project into the lumen of the alimentary tract; they possess large nuclei and the sides of the cells facing the lumen have a distinct striated appearance, which is absent in those epithelial cells covered with a chitinous intima. This striated appearance may be related in some way to the production of the mucous intima which is generally present in the ventriculus, and which appears to take the place of the loose chitinous intima or peritrophic

membrane which occurs in this region in numerous insects, and which has been studied in detail by Vignon (1901) and others. Below the epithelial cells a number of small cells (*g. c.*) are found, which may be either gland cells or young epithelial cells. In addition to these cells small groups of deeply-staining fusiform cells (*i. c.*) are found below the epithelium. These, I believe, are embryonic cells from which the mesenteron of the imago arises. The Malpighian tubes arise in the tenth segment at the junction of the ventriculus and the intestine.

The intestine (fig. 29, *int.*) is narrower than the ventriculus and runs forwards as far as the eighth segment, where it bends below the visceral mass and runs posteriorly, to become dorsal again behind the tenth segment, from whence it runs backwards, turning ventrally behind the visceral mass to become the rectum. The epithelium is thrown into a number of folds and is covered with a chitinous intima.

The rectum (*r.*) is very short and muscular, and the chitinous intima is fairly thick and continuous with the outer cuticular layer of the chitinous integument. It is almost vertical and opens by the anus on the ventral side of the terminal larval segment between the two swollen anal lobes.

Salivary glands.—There is a pair of large tubular salivary glands (*s. gl.*) lying laterally in segments five and six. Anteriorly each is continued as a tubular duct; the two ducts approach each other and join beneath the pharyngeal mass to form a single median duct (fig. 19, *sal. d.*) which runs forward and opens into the pharynx on the ventral side as already described. The glands are composed of large cells (fig. 21), which project into the lumen of the gland; they stain deeply and have large active nuclei. The salivary secretion, apart from the digestive properties which it has, is no doubt of great importance in making the food more liquid, as is also the case in the imago, and so rendering it more easy for absorption.

The Malpighian tubes (fig. 29, *m. t.*) arise at the junction of the ventriculus and intestine in the tenth segment. A short

distance from their origin they bifurcate and the resulting four tubules have a convoluted course, being mingled to a great extent with the adipose tissue. They are similar in appearance and histologically to those of the imago, consisting of large cells, of which only two can be seen usually in section; they consequently give the tubules a moniliform appearance. In the mature larva these cells appear to break down to form small deeply-staining spherical bodies. This histological degeneration begins at the distal ends of the tubules, which in the mature larva usually have the appearance shown in fig. 28 (*m. t.*); all the stages of degeneration can be traced out. This process may be a means of getting rid of the remaining larval excretory products.

The four cæca at the anterior end of the ventriculus have already been described.

## 5. THE RESPIRATORY SYSTEM.

The tracheal system (fig. 26) of the adult larva consists of two longitudinal tracheal trunks united by anterior and posterior commissures, and communicating with the exterior by anterior and posterior spiracles, the latter are situated in the middle of the oblique caudal end, and the anterior spiracles, which are not present in the first larval instar, are situated laterally at the posterior border of the third body-segment.

I believe that the anterior spiracles (*a. sp.*) are true functional spiracles, though for some time I shared Lowne's opinion that they were not functional. This latter view was due to the fact that it was difficult to understand how these spiracles could obtain air when they are immersed, as they usually are, in the moist fermenting materials on which the animal feeds. A careful examination of their structure, however, strengthens my belief that they are able, if necessary, to take in air; the occasions when this is possible are probably not infrequent. Each of the anterior spiracular processes consists of a fan-shaped body (fig. 9, *a. sp.*) bearing six to eight small papilliform processes. The papillæ (fig. 7)

open to the exterior by a small pore which leads into a cavity having a clear lumen surrounded by branched cuticular processes, whose function is probably to prevent solid particles from penetrating the spiracular channel. The body of the fan-shaped spiracular process is filled with a fine reticulum of the chitinous intima, which Meijere (1902) calls the "felted-chamber" (Filzkammer); through this meshwork the air can pass to the longitudinal tracheal trunk.

The posterior spiracles (fig. 3, *p. sp.*) are D-shaped with the corners rounded off and their flat faces are opposed. Each consists of a chitinous ring having internal to the flat side a small pierced knob. Each chitinous ring encloses three sinuous slits, guarded by inwardly-directed fine dendritic processes; through these slits the air enters the small spiracular atrium, one of which is situated internal to each of the spiracles. The spiracular atria communicate directly with the longitudinal tracheal trunks.

The course and origin of the branches of each of the longitudinal tracheal trunks (fig. 26 *l. tr.*) is the same, so that of the left side will be described only. Immediately behind the spiracular atria the short posterior tracheal commissure (*p. com.*) connects the two trunks. In the younger larvæ this commissure is situated more anteriorly, but in the adult it is situated so far back and so close to the spiracles that its presence might easily be overlooked. On the outer side of the tracheal trunk a large branch arises; this, the visceral branch (*v. tr.*), bends ventrally to the lateral trunk, and thus becoming internal to it enters the convoluted visceral mass with its fellow of the other side. The visceral branches extend anteriorly as far as the seventh segment. In the twelfth and thirteenth segments the lateral tracheal trunk has a double appearance. A dorsal and a ventral branch arise in most of the segments, the dorsal branch chiefly supplies the fat body, and the ventral branch supplies the viscera; both give off branches to the muscular body wall. The anterior commissure (*a. com.*) is situated in the fourth segment. It crosses the oesophagus immediately behind the pharyngeal mass. On



the internal side of the portion of the lateral tracheal trunk that is anterior to the commissure a branch arises, and running ventral to the pharyngeal mass it supplies the anterior end of the larva and the oral lobes. A branch that supplies the muscles of this region is given off external to the origin of the anterior commissure. Internal to the origin of the commissure two tracheæ arise; the anterior branch enters and supplies the pharyngeal mass, and the posterior branch (*tr.*') enters the ganglion ventral to the cerebral lobes. In the fifth segment another internal tracheal branch enters the ganglion (*tr.*''). These tracheæ which supply the ganglion appear to run chiefly in the peripheral regions, where they divide into a number of branches, the fate of some of these being interesting. These branches are extremely fine, and they arise, as I have previously mentioned, in association with a number of the segmental nerves with which they run to the body wall.

## 6. THE VASCULAR SYSTEM AND BODY CAVITY.

The relations and structure of the vascular system of the larva are on the whole similar to those of the fly; there are, however, a number of modifications.

The dorsal vessel, which includes the so-called "heart," is a simple muscular tube lying on the dorsal side immediately beneath the skin, and extending from the posterior tracheal commissure to the level of the cerebral lobes of the compound ganglion in the fifth segment. Its wall is composed of fine striated muscle-fibres arranged transversely and longitudinally, but chiefly in the latter direction. The swollen posterior region (Pl. 33, fig. 31), which is called the heart, lies in the last three or four segments, its anterior limit being hard to define. It consists of three distinguishable chambers, which, however, are not divided by septa. Three pairs of ostia (*os.*), each provided with a pair of internal valves (*v.*), are situated laterally, and place the cardiac cavity in communication with the pericardium, in which this portion of the dorsal vessel lies. There are three pairs of alar muscles controlling the



action of this posterior eardiae region of the dorsal vessel. Lowne describes other openings in the wall of the "heart" of the blow-fly larva, but I have been unable to find others than those already described in this larva; it has three pairs only.

The dorsal aorta is the anterior continuation of the dorsal vessel, which gradually diminishes in diameter. When it reaches the fifth segment and lies above the ganglion, it terminates in a peculiar cellular structure (fig. 24, *c. r.*), which in the blow-fly has a circular shape and was called by Weismann the "ring." In the larva of *M. domestica* it has not so pronounced a ring-like appearance, but is more elliptically compressed and rather  $\Lambda$ -shaped. The cells of which it is composed have a very characteristic appearance, and are rather similar to a small group of cells lying on the neck of the proventriculus and at the anterior end of the dorsal vessel of the fly. From the lower sides of this cellular structure (fig. 28, *c. r.*) the outer sheaths of the major cephalic imaginal discs depend, and extend anteriorly to the pharyngeal mass, enclosing between them the anterior portion of the great ventral blood sinus.

The pericardium lies in the four posterior segments of the body, and is delimited ventrally from the general body-cavity by a double row of large characteristic pericardial cells. These cells have a fine homogeneous structure and are readily distinguished from the adjacent adipose tissue cells, whose size they do not attain. The pericardial cavity contains a profuse supply of fine tracheal vessels which indicates a respiratory function. A similar condition occurs in the blow-fly larva, and Imms (1907) has described a rich pericardial tracheal supply in the larva *Anopheles maculipennis*, as also Vaney (1902) and Dell (1905) in the larva of *Psychoda punctata*. The adipose tissue cells (fig. 28, *f. c.*) form the very prominent "fat-body." They are arranged in folded cellular laminae that lie chiefly in the dorso-lateral regions of the body, and in section have the appearance shown in the figure. The cells have a similar structure to those of the adult fly; they are

very large, with reticular protoplasm containing fat globules, and there may be more than one nucleus in a single cell. As in the fly, the fat-body is closely connected with the tracheal system by means of a very rich supply of tracheæ.

Two chief blood-sinuses can be distinguished—the pericardial sinus, which has already been described, lying in the dorsal region in the four posterior segments, and the great ventral sinus. The latter lies between the outer sheaths of the major cephalic imaginal discs and extends anteriorly into and about the pharynx; posteriorly it encloses the ganglion and the convoluted visceral mass, above which it opens into the pericardial sinns between the pericardial cells.

The blood which fills the heart and sinuses and so bathes the organs is an almost colourless, quickly coagulable fluid, containing colourless, nucleated, amœboid corpuscles and small globules of a fatty character.

## 7. THE IMAGINAL DISCS.

As in other cyclorrhaphic Diptera, the imaginal discs of some of which have been described by Weismann (1864), Kunckel d'Herculais (1875-78) and Lowne, the imago is developed from the larva by means of these imaginal rudiments, which are gradually formed during the later portion of the larval life. They do not all appear at the same time, for whereas some may be in a well-developed state early in the third larval instar, others do not appear until the larva reaches its resting period or even later. The imaginal discs appear to be hypodermal imaginations though their origin is difficult to trace in all cases; in many instances they are connected with the hypodermis by means of a stalk of varying thickness. The imaginal disc or rudiment may consist of a simple or of a folded lamina of deeply-staining columnar embryonic cells, as in the wing discs, or of a number of concentric rings of these cells, as in the antennal and crural discs. They are usually closely connected with the tracheæ and in some cases are innervated by fine nerves. Although the imaginal discs

of *M. domestica* are similar in some respects to those of the blow-fly, as described by Lowne, there are several important differences, chief of which is the position of the imaginal discs of the meta-thoracic legs.

During the resting period of the larva the cephalic and thoracic discs can be distinguished, but the abdominal discs are small and not so obvious except in sections.

The cephalic discs.—The chief cephalic discs are contained in what at first appears to be a pair of cone-shaped structures in front of each of the cerebral lobes of the ganglion (fig. 24, *m.c.d.*); the cone, however, is not complete. The outer sheath of each of these major cephalic imaginal rudiments is continued dorsally, and joins the eellular structure mentioned previously (see fig. 28), thus enclosing a triangular space which is a portion of the ventral sinus. These sheaths are continued anteriorly and are connected to the pharyngeal mass, and it is through this connecting strand of tissue that the discs are everted to form the greater part of the head of the nymph. Immediately in front of the cerebral lobe is the so-called optic disc (fig. 27, *o.d.*), which in its earlier stages is cup-shaped, but later it assumes a conical form, having a cup-shaped base adjacent to the cerebral lobe. The optic disc is connected to the cerebral lobe laterally by a stalk of tissue, the optic stalk (*o.s.*), which becomes hollow later, and it is through this stalk that the optic ganglion and associated structures contained in the cerebral lobe appear to evaginate when the final metamorphosis and eversion of the imaginal rudiments takes place. The optic discs form the whole of the lateral regions of the head of the fly. The remaining portion of the head-capsule of the fly is formed from two other pairs of imaginal rudiments, the antennal and facial discs. The antennal disc (*an.d.*) lies in front of, and internal to, the optic discs. Each consists of an elongate conical structure, in which at a later stage the individual antennal joints can be distinguished. The facial discs (*f.d.*) are anterior to the antennal discs and extend to the anterior end of the conical structure containing these

three pairs of major cephalic discs, which will form the cephalic capsule.

In addition to these two other pairs of cephalic discs are found. A pair of small flask-shaped maxillary rudiments are situated one at the base of each of the oral lobes; a second pair of imaginal discs, similar in shape to the maxillary discs, is found adjacent to the hypostomal sclerite; the latter, I believe, are the labial rudiments, and will form almost the whole of the proboscis of the fly.

The thoracic discs.—In *M. domestica* there are five pairs of thoracic discs. The pro-thoracic imaginal discs (figs. 24 and 28, *pr. d.*) are attached to the anterior end of the ganglion and slope obliquely forwards; the distal end of each is attached to the body-wall on the ventral side between segments three and four. These discs develop into the pro-thoracic legs, and probably also into the much reduced pro-thoracic segment, as I was unable to discover any other rudiments corresponding to the dorsal imaginal discs of the meso-thoracic and meta-thoracic segments. Arising from the sides of the ganglion immediately behind the attachment of the pro-thoracic rudiment are the imaginal rudiments of the meso-thoracic legs and sternal region (*v. ms.*); the distal stalks of this pair of imaginal discs are attached to the body-wall at the posterior border of the fourth segment. The dorsal meso-thoracic imaginal discs, from which originate the mesonotal region and the wings, may be termed the alar or wing discs. They form a pair of flattened pyriform saca (fig. 22, *d.ms.*), lying one on each side of the ventral side of the fifth segment and slightly external to the lateral tracheal trunk (fig. 28, *d.ms.*), to a ventral branch of which each is attached. The meta-thoracic discs consist of two pairs of small pyriform masses (fig. 22) lying immediately behind the alar discs in the intersegmental line. They are attached to a ventral branch of the lateral tracheal trunk. The anterior rudiment (*r. mt.*) is the larger, and forms the imaginal meta-thoracic leg and sternal region; in the blow-fly and *Volucella* it is interesting to note that this pair of imaginal discs is situated further

forward, and is in association with the corresponding pro-thoracic and meso-thoracic ventral discs. The smaller and more posterior disc (*d. mt.*) will develop into the remaining portion of the much reduced meta-thoracic segment, including the halteres.

Reference has already been made to other imaginal rudiments which occur in the abdominal region as circular patches of embryonic cells. The abdominal segments develop from numerous segmentally arranged plates of a similar nature, which are found during the early pupal stage.

During pupation the imaginal rudiments increase in size and are not destroyed by the phagocytes in histolysis, as is the case with most of the larval structures. The cephalic discs are evaginated by the eversion of their sacs by way of the anterior end of the larva, a cord of cells attached to the dorsal wall of the anterior end of the pharynx marking the path of eversion. A similar process takes place in the case of the thoracic imaginal discs, which, by their eversion, build up the whole of the skeletal case of the thorax and its dorsal and ventral appendages, the wings, halteres and legs.

## VI. SUMMARY.

1. An account of the previous work on the breeding habits of *M. domestica* is given, which, together with the author's investigations, show that the house-fly breeds in the following substances :

Horse-manure; this is preferred by the female flies as a nidus for the eggs, and forms the chief substance in which they breed; human excrement, either in the form of isolated faeces or occurring in such places as latrines, privies and ash-pits; cow-dung; poultry excrement; also in substances contaminated or mixed with excremental products, such as bedding from piggeries and from rabbits and guinea-pigs, paper and textile fabrics which have been contaminated, as cotton and woollen garments, sacking, rotten flock-beds, straw-mattresses, cesspools; decaying vegetable substances



such as vegetable refuse from kitchens and decaying grain; rotten fruit, as bananas, apricots, cherries, plums, peaches and melon-slices; in spent hops; in waste food-stuffs, as bread moistened with milk, boiled egg, broth; bad meat and dead animals.

2. The most important factor in the development is temperature; a high temperature accelerates the development. Other factors concerned in the development are—the nature of the food and moisture, the effects of which are shown. Fermentation is also an important factor in development, as first shown by de Geer.

3. The shortest time occupied in the development, that is, from the deposition of the egg to the exclusion of the imago, is eight days, which period is obtained when the larvæ are incubated at a constant temperature of about 35° C.; under unfavourable conditions the development may extend over several weeks.

4. There are three larval stages, and the shortest times obtained for the development of the different developmental stages is—egg, from deposition to hatching, eight hours; first larval instar, twenty hours; second larval instar, twenty-four hours; third larval instar, three days; pupal stage, three days.

5. House-flies usually breed from June to October, but if the necessary conditions of temperature and suitable food are present they are able to breed practically the whole year round; these conditions are not, as a rule, satisfied during the winter months, except in such places as warm stables, etc.

6. The flies become sexually mature in ten to fourteen days after their emergence from the pupa, and they may begin to deposit their eggs as early as the fourteenth day after emergence. Each fly lays from 120–150 eggs in a single batch, and it may lay as many as six batches during its life.

7. The anatomy of the adult larva is described in the second portion of the paper. The body of the larva is considered to be composed of thirteen segments, of which the remnant of the cephalic region or pseudo-cephalon forms the



first. The apparant single second segment is considered to be of a double nature.

8. The muscular system is described in detail. It consists of: (1) A segmentally-arranged series of flattened cutaneous muscles forming an almost perfect sheath below the hypodermis; (2) the muscles controlling the cephalo-pharyngeal sclerites and pharynx; (3) the cardiac and visceral muscles. The series of muscular actions which probably takes place during locomotion is described.

9. The central nervous system is concentrated to form a single compound ganglion in which eleven pairs of component ganglia can be recognised. On the dorsal side of the anterior end of the ganglion two cerebral lobes united in the median line above the œsophageal foramen are situated; these contain the rudiments of the optic and supra-œsophageal ganglionic structures of the fly. Eleven pairs of segmental nerves arise from the ganglion, and in addition to these three pairs of lateral nerves, and also a single pair and two median unpaired dorsal accessory nerves arise. The component ganglia are surrounded by a cortical layer containing large ganglion cells; the whole compound ganglion is enclosed in a capsular sheath.

The only sensory organs are two pairs of tubercles situated on the dorsal sides of the oral lobes. By their structure they indicate an optical function.

10. The alimentary tract is very long in the larva, the ventriculus being especially elongate. It consists of pharynx, œsophagus, proventriculus, ventriculus, intestine and rectum. In addition to a pair of salivary glands, whose ducts unite to open by a single duct at the anterior end of the pharynx, and a pair of bifurcating Malpighian tubes, the larva possesses four cæca at the anterior end of the ventriculus. The ventriculus and intestine are very convoluted and are coiled up to form a complicated visceral mass.

11. The tracheal system of the adult larva consists of two longitudinal lateral tracheal trunks united by anterior and posterior commissures, and communicating with an exterior

by means of an anterior and a posterior pair of spiracles. The anterior spiracles, which do not occur in the first larval instar, are considered to be functional.

12. The vascular system consists of: (1) A dorsal vessel, the posterior region of which is swollen to form a cardiac region or "heart" which communicates with a pericardial cavity by means of three pairs of lateral ostia; (2) the great ventral sinus, which forms the body cavity; and (3) the pericardial sinus. The pericardium is well supplied with tracheæ, which may assist in respiration, as in certain other insect larvæ. The adipose tissue cells which compose the large laminae forming the fat-body are similar in structure to those of the fly.

13. Three groups of imaginal rudiments or discs can be recognised in the larva: (1) The cephalic discs, of which two appendicular pairs are situated at the anterior end of the larva and three pairs in front of the cerebral lobes of the ganglion; (2) the thoracic discs, two pairs of which are attached to the anterior end of the ventral side of the ganglion, and three pairs are connected with the lateral tracheal trunks in the fifth segment; (3) the abdominal and visceral discs.

## VII. LITERATURE.

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## EXPLANATION OF PLATES 30—33,

Illustrating Mr. C. Gordon Hewitt's paper on "The Structure, Development, and Bionomics of the House-fly *Musca domestica*, Linn. Part II. The Breeding Habits Development and the Anatomy of the Larva."

### PLATE 30.

FIG. 1.—Eggs of *M. domestica*,  $\times 40$ , dorsal and dorso-lateral views.  
*a.* Anterior end.

FIG. 2.—Egg immediately before emergence of the larva which can be seen through the dorsal split of the chorion through which it emerges.

FIG. 3.—Posterior end of mature larva (3rd instar).  
*an.* Anus. *p.sp.* Posterior spiracle.

FIG. 4.—Cephalopharyngeal skeleton of mature larva, left lateral aspect.  
*d.p.s.* Dorsal pharyngeal sclerite. *d.s.* Dentate sclerite, *h.s.* Hypostomal sclerite. *l.p.* Lateral pharyngeal sclerite or plate, deeply incised posteriorly to form dorsal and ventral processes. *m.s.* Mandibular sclerite.

FIG. 5.—Mature larva of *M. domestica*.  
*a.sp.* Anterior spiracular process. *an.l.* Anal lobe. *sp.* Spiniferous pad. I—XIII. Body segments.

FIG. 6.—Ventral aspect of the Pseudocephalon and second body segment of the mature larva showing the two oral lobes traversed by the food channels.  
*l.* Lingual-like process. *m.* Mouth. *m.s.* Mandibular sclerite. *o.t.* Anterior optic tubercle.

FIG. 7.—Transverse section through two of the papillæ of the anterior spiracular process to show the clear central lumen.  
*c.p.* The cuticular processes.

FIG. 8.—Larva shortly after hatching (1st instar).  
*m.s.* Mandibular sclerite. *p.sp.* Posterior spiracle raised on short tubercle. *sp.* Spiniferous pad.

FIG. 9.—Lateral (left) aspect of the anterior end of the mature larva.  
 I—IV. Body segments. *a.sp.* Anterior spiracular process showing seven spiracular papillæ. *m.s.* Mandibular sclerite. *o.t.* Optic tubercle. *ps.* Pseudocephalon.



FIG. 10.—“Nymph” of *M. domestica* dissected out of pupal case about 30 hours after pupation.

*an.* Swellings of nymphal sheath marking bases of antennæ. *cx.* Coxa of leg. *lb.* Labial portion of proboscis sheath. *lbr.* Labral portion of same. *n.sp.* Spiracular process of nymph. *w.* Wing in nymphal alar sheath.

FIG. 11.—Head of “nymph” (about 48 hours after pupation). Enclosed in nymphal sheath. To show the development of the imaginal proboscis.

*an.* Antenna. *c.e.* Compound eye. *fac.* Facialia. *lab.* Labrum. *mx.p.* Maxillary palp. *o.l.* Oral lobe.

FIG. 12.—Posterior end of larva in the second stage (2nd instar).

*an.* Anus. *p.sp.* Posterior spiracle.

FIG. 13.—Cephalopharyngeal skeleton of the first larval instar; the outline of the pharyngeal mass is shown in dotted lines.

*t.s.* T-shaped sclerite of the left oral lobe. Other lettering as in Fig. 4.

FIG. 14.—Longitudinal section through the surface of one of the oral lobes of mature larva to show the food-channels.

*ch.* Food-channel. *ct.* Outer layer of cuticular integument. *ct'.* Inner layer of the same. *hy.* Hypodermis.

FIG. 15.—Pupal case of *M. domestica* from which the imago has emerged, thus lifting off the anterior end or “cap” of the pupa; ventro-lateral aspect.

*a.sp.* Remains of the anterior spiracular process of larva. *l.tr.* Remains of the larval lateral tracheal trunk. *n.sp.* Temporary spiracular process of nymph. *p.sp.* Remains of the posterior spiracles of larva.

### PLATE 31.

FIG. 16.—Muscular system of the body-wall of the right side. The straight dorsal line is the median dorsal line of the body, and the curved ventral line is the median ventral line.

I—XIII. Body segments. *an.l.* Anal lobe. *an.m.* Anal muscle. *c.r.* Cephalic retractor muscle. *d.v.* Dorso-ventral muscle of the terminal segment. *ex.d.l.* External dorso-lateral oblique recti muscles. *i.l.o.* Internal lateral oblique muscle. *in.d.l.* Internal dorso-lateral oblique recti muscles. *l.i.m.* Lateral intersegmental muscle. *l.m.* Lateral muscles. *l.tr.* Branch of lateral tracheal trunk communicating with the anterior spiracular process. *l.v.l.* Longitudinal ventro-lateral muscles. *p.sp.* Posterior spiracle. *s.d.* Stomal dilators. *v.c.r.*, *v'.c.r.* Ventral cephalic retractor muscles. *v.l.o.* Ventro-lateral oblique muscle. *v.o.* Ventral oblique muscle.

FIG. 17.—Oblique section through the pharyngeal mass of the larva in the direction and at the level shown by the line *a.b.* in Fig. 19. (Camera lucida drawing.)

*e.o.m.* Elongate oblique pharyngeal muscle. *l.p.* Lateral pharyngeal



## STRUCTURE, DEVELOPMENT, AND BIONOMICS OF HOUSE-FLY. 543

sclerite. *m.* Accommodating membrane. *m.d.* Mandibular depressor muscle. *o.ph.* Oblique pharyngeal muscle. *ph.* Pharynx. *s.d.m.* Semicircular dorsal pharyngeal muscles. *tr.* Trachea. *v.c.p.* Ventral cephalic protractor muscle.

FIG. 18.—Oblique section through the pharyngeal mass of the larva at the level shown by the line *x.y.* in Fig. 19. (Camera lucida drawing.)

*p.s.* Pharyngeal sinus. *r.ph.* Roof of pharynx. *T.r.* T-ribs of the floor of pharynx. Other lettering as in Figs. 17 and 19.

FIG. 19.—Muscles of the cephalo-pharyngeal sclerites of the mature larva seen from the left side. The muscles of the body-wall have been omitted with the exception of the large cephalic retractor muscles.

*a.b., x.y.* Levels and direction of the oblique sections shown in Figs. 18 and 19. *c.r.* Cephalic ring. *d.c.p.* Dorsal cephalic protractor muscle. *d.m.* Right pharyngeal depressor muscle. *d.s.* Dentate sclerite. *f.p.* Chitinous floor of the posterior region of the pharynx showing the bases of the T-ribs. *h.s.* Hypostomal sclerite. *m.d.* Mandibular depressor muscle. *m.e.* Mandibular extensor muscle. *m.s.* Mandibular sclerite. *s.d.* Stomal dilator muscles. *sal.d.* Common salivary duct. *v.c.p.* Ventral cephalic protractor muscles. *v.c.r.* and *v'.c.r.* Ventral cephalic retractor muscles.

FIG. 20.—Visceral or stomatogastric nervous system of the mature larva. The position of the ganglion (*G.*) with the cerebral lobes (*c.l.*) is shown by means of the dotted outline.

*c.g.* Central visceral ganglion. *pv.g.* Proventricular or posterior ganglion.

FIG. 21.—Transverse section of one of the salivary glands of the mature larva. (Camera lucida drawing.)

FIG. 22.—Internal aspect of the posterior thoracic imaginal discs of the right side.

*d.ms.* Dorsal mesothoracic or alar imaginal disc. *d.ml.* Dorsal metathoracic imaginal disc. *l.tr.* Lateral tracheal trunk of the right side of larva. *v.ml.* Ventral metathoracic imaginal disc.

## PLATE 32.

FIG. 23.—Nervous system of the mature larva. The dorsal accessory nerves are shown by single black lines, and the outline of the pharyngeal mass is indicated by the dotted line.

I—XII. Body segments of the larva. *c.l.* Cerebral lobes. *m.c.d.* Major cephalic imaginal discs. *æ.* Œsophagus. *o.v.* Anterior (œsophageal branch) of visceral nervous system.

FIG. 24.—Left lateral aspect of the ganglion of the mature larva showing the origin of the nerves, position of the imaginal discs, and anterior end of the dorsal vessel.

1—11. Eleven segmental nerves. *a.b.* and *c.* Nerves arising from the bases

of the stalks of the prothoracic and ventral mesothoracic imaginal discs. *c.l.* Cerebral lobe. *c.r.* Problematical cellular structure (Weismann's "ring").

*d.a'*, *d.a''*, *d.a'''*. Dorsal accessory nerves. *d.v.* Dorsal vessel. *m.c.d.* Major cephalic imaginal discs. *œ.* Œsophagus. *pr.d.* Prothoracic imaginal disc. *l.* Fine tracheæ which arise in association with the segmental nerves, others arise with some of the more posterior nerves, but for the sake of clearness they are not included in the figure. *tr'*, *tr''*. Tracheæ entering the ganglion. *v.m.s.* Ventral mesothoracic imaginal disc. *v.n.* Visceral nerve.

FIG. 25.—Longitudinal section of the proventriculus of the mature larva (Camera lucida drawing.)

*c.c.* Large cells forming the central hollow core of the proventriculus. *ch.i.* Chitinous intima of the œsophagus. *e.v.* Epithelial cells continuous with and similar in character to those of the ventriculus. *i.c.* Ring of imaginal cells. *œ.ep.* Œsophageal epithelial cells. *v.c.* Lumen of ventriculus.

FIG. 26.—The longitudinal lateral tracheal trunk of the left side seen latero-dorsally showing the origin of the tracheal branches; small portions only of the right trunk are shown.

*a.com.* Anterior tracheal commissure. *a.sp.* Anterior spiracular process. *f.b.* Fat-body. *or.l.* Oral lobe. *l.tr.* Longitudinal lateral tracheal trunk. *p.com.* Posterior commissure. *p.sp.* Posterior spiracle. *tr'*. Trachea entering ganglion anteriorly. *tr''*. Trachea entering ganglion laterally. *v.tr.* Visceral tracheal trunk.

FIG. 27.—Longitudinal sections through the major cephalic imaginal discs of mature larva to show the position of the individual imaginal rudiments. The dextral section is more dorsal than the sinistral. (Camera lucida drawings.)

*an.d.* Imaginal disc of the antenna. *f.d.* Facial imaginal disc. *i.s.* Sheath of imaginal rudiments. *o.d.* Optic imaginal disc. *o.g.* Imaginal disc of the optic ganglionic structures. *o.s.* Optic stalks. *s.g.* Fundament of the imaginal supra-œsophageal ganglionic. *sh.* Sheath of cerebral lobe.

FIG. 28.—Transverse section of mature larva anterior to the ganglion and cerebral lobes to show the position of certain of the imaginal discs. The body-wall and muscles have been omitted. The folded character of the adipose tissue laminae can be seen in this section, and also the degenerating anterior portions of the malpighian tubules (*m.t.*). (Camera lucida drawing.)

*an.d.* Antennal disc. *c.r.* Problematical cellular structure (Weismann's "ring"). *c.v.* Cæcum of ventriculus. *d.ms.* Dorsal mesothoracic (alar) imaginal disc. *f.c.* Adipose tissue cell. *l.tr.* Lateral tracheal trunk. *m.t.* Malpighian tubule cut rather longitudinally. *œ.* Œsophagus. *pr.d.* Prothoracic imaginal disc. *v.ms.* Ventral mesothoracic imaginal disc.

## PLATE 33.

FIG. 29.—Alimentary system of mature larva. The course of the ventriculus and intestine as they lie in the larva is shown by the dotted lines. The origins only of the Malpighiau tubes are shown.

*c.s.d.* Common salivary duct. *c.v.* Cæcum of ventriculus. *int.* Intestine. *m.t.* Malpighian tubule. *œ.* Œsophagus. *ph.* Pharynx. *pv.* Proveutriculus. *r.* Rectum. *s.gl.* Salivary gland. *v.* Ventriculus.

FIG. 30.—Transverse section of a portion of the ventriculus of mature larva. (Camera lucida drawing.)

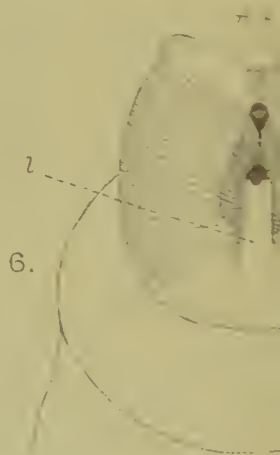
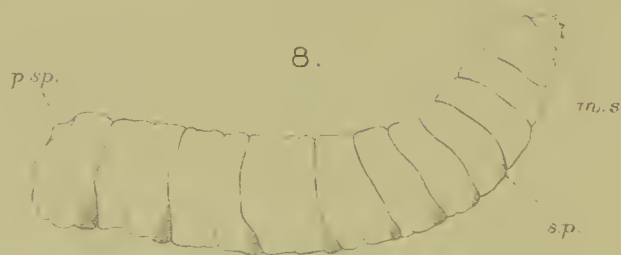
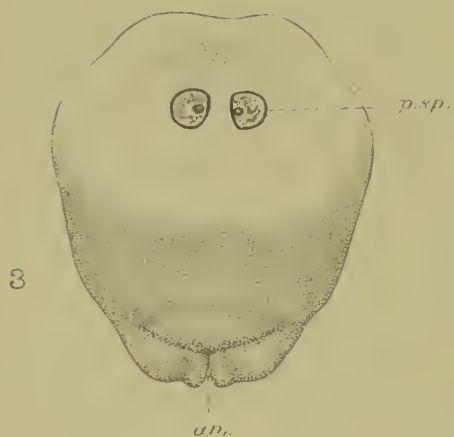
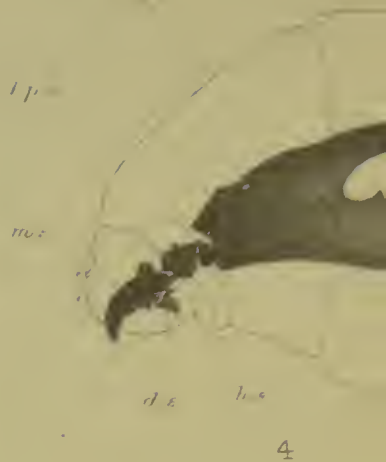
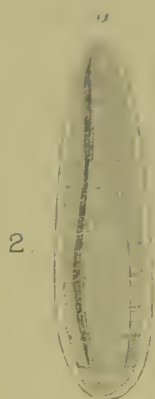
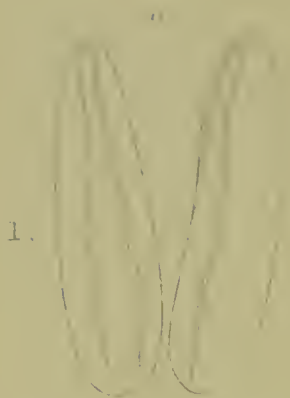
*e.v.* Epithelial cell of ventriculus showing large active nucleus and striated peripheral region of cell. *g.s.* Probable gland cells. *i.c.* Group of imaginal cells.

FIG. 31. Horizontal section of posterior or “cardiac” region of the dorsal vessel. (From camera lucida drawings.)

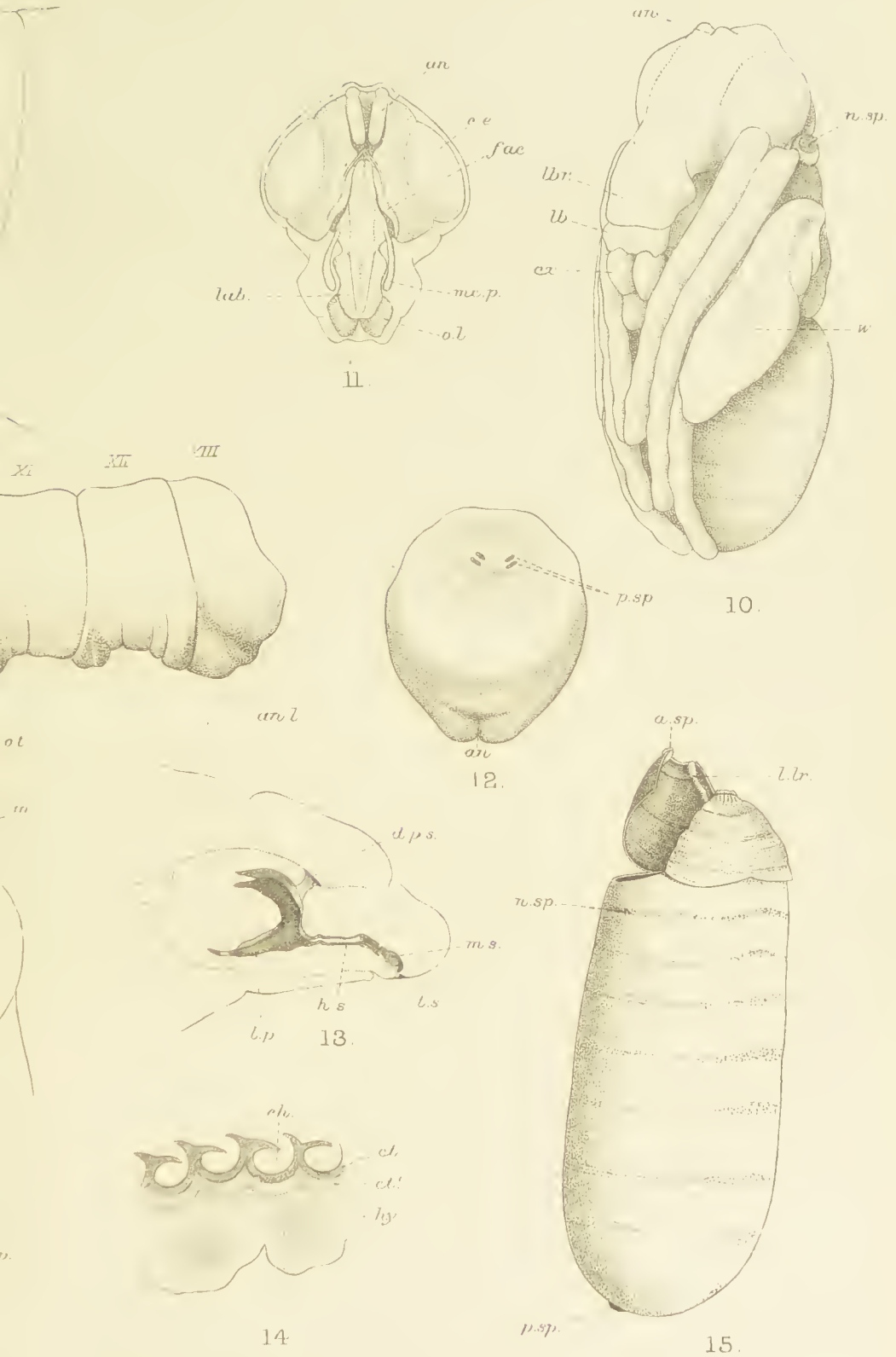
*os.* Ostium. *v.* Valvular flaps guarding the same.





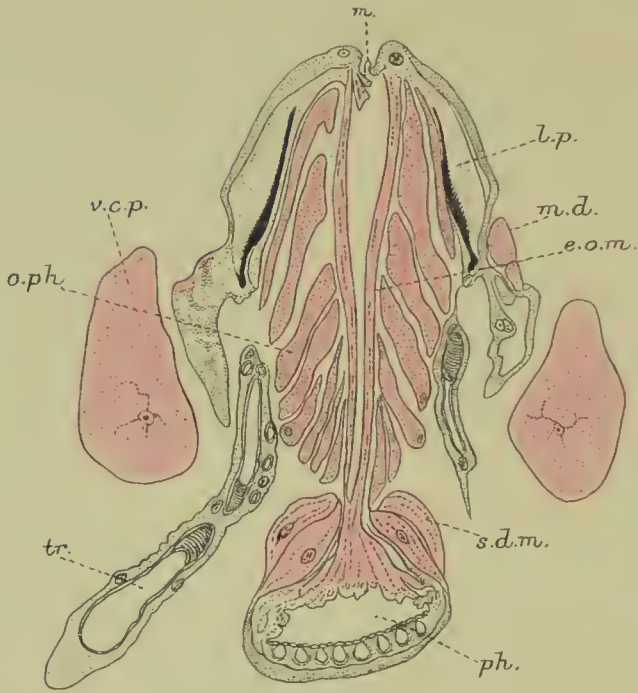
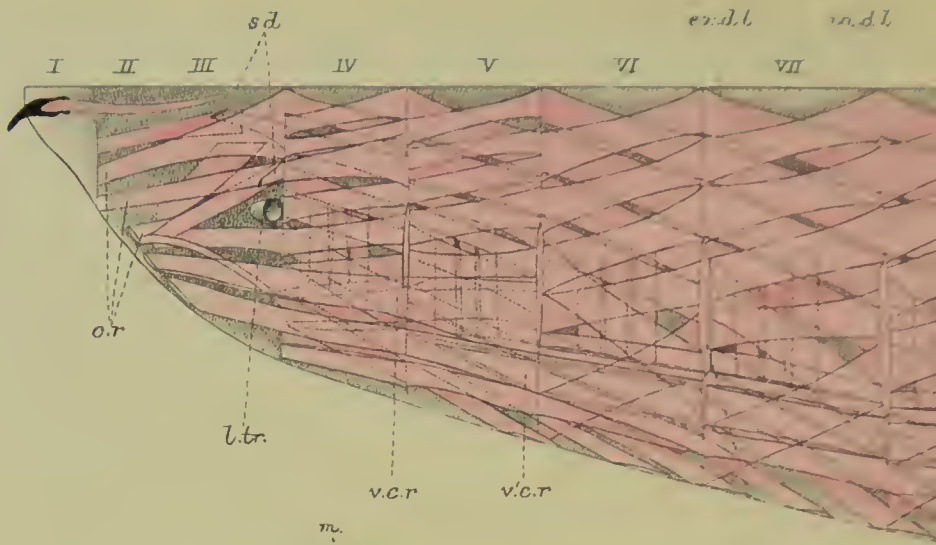




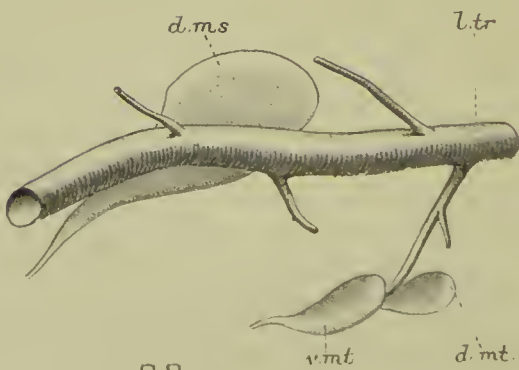




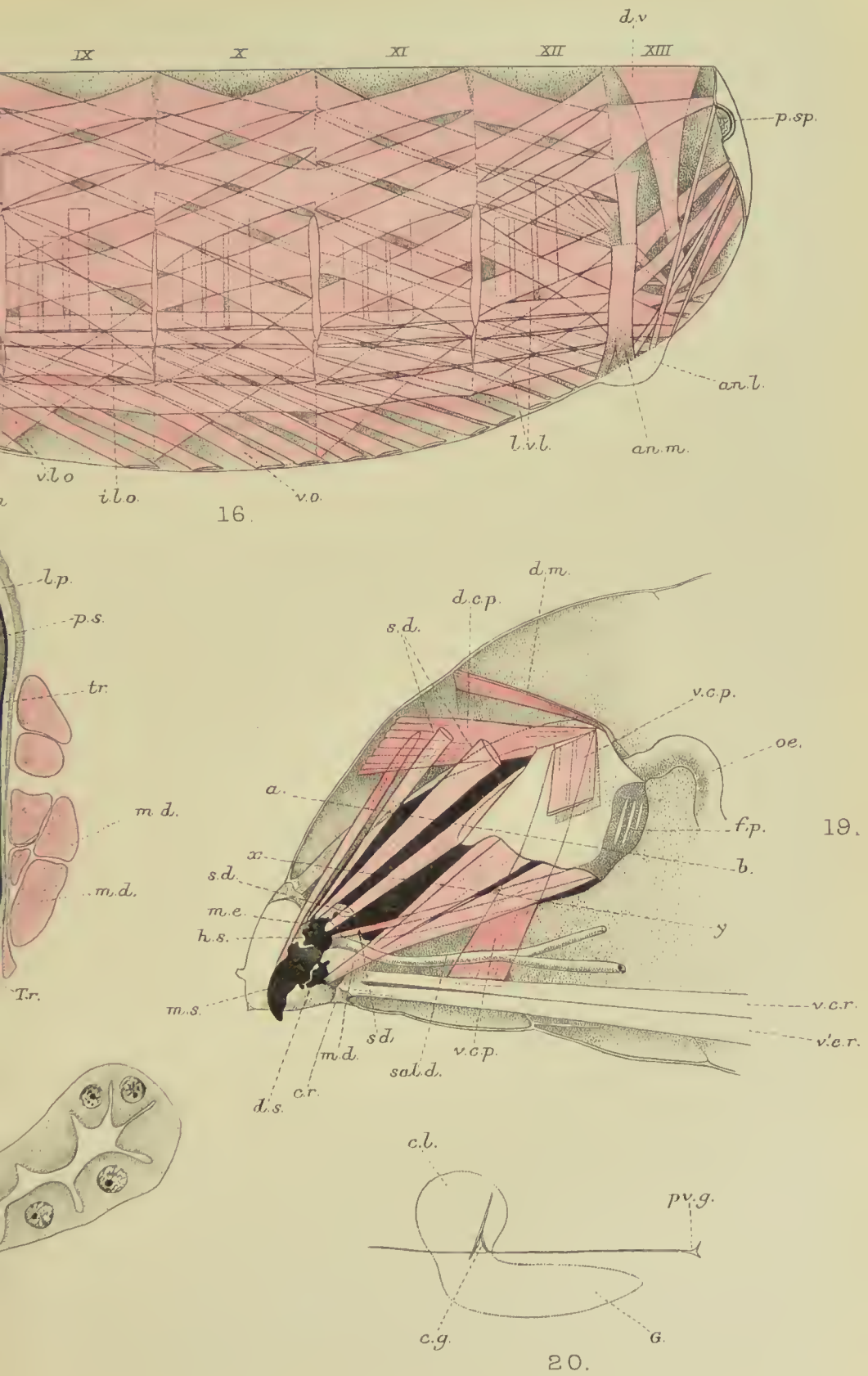




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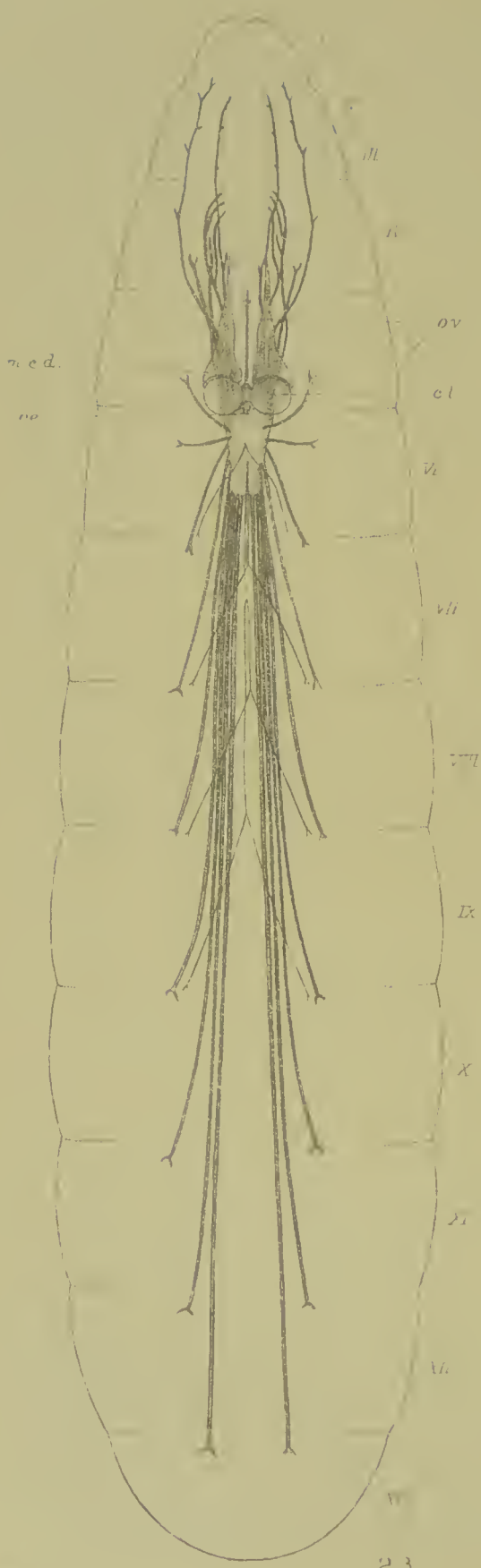
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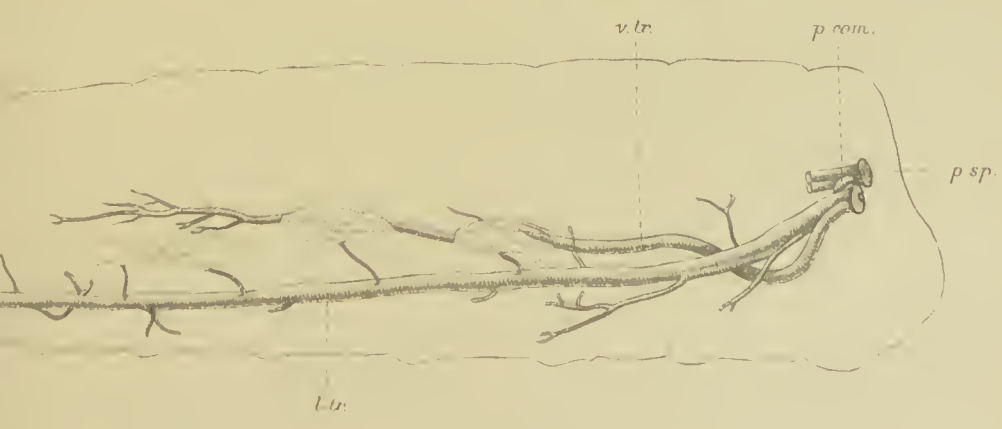
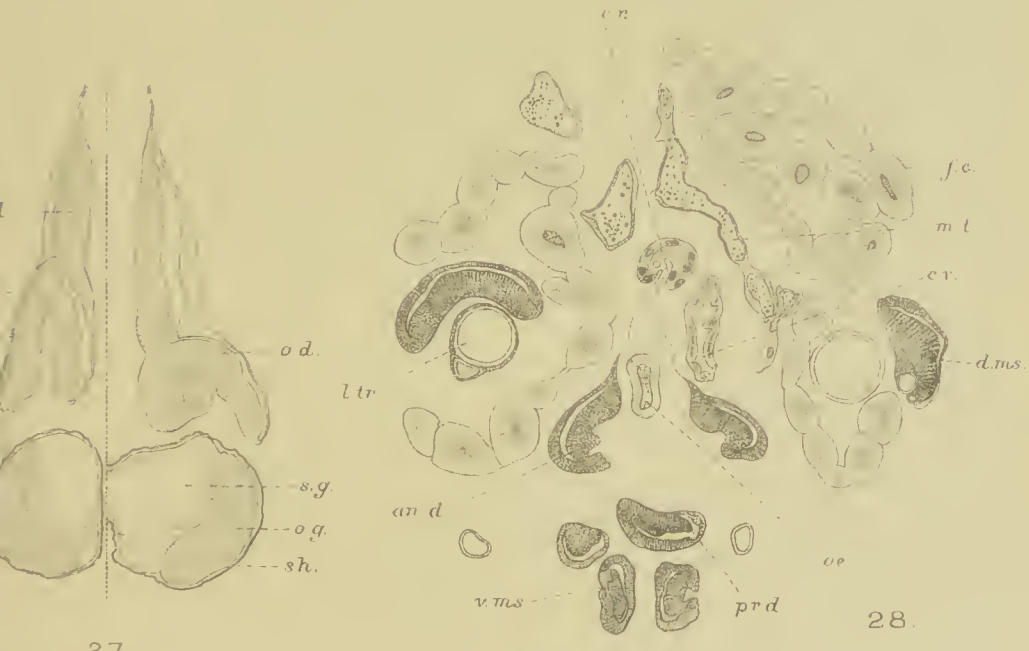
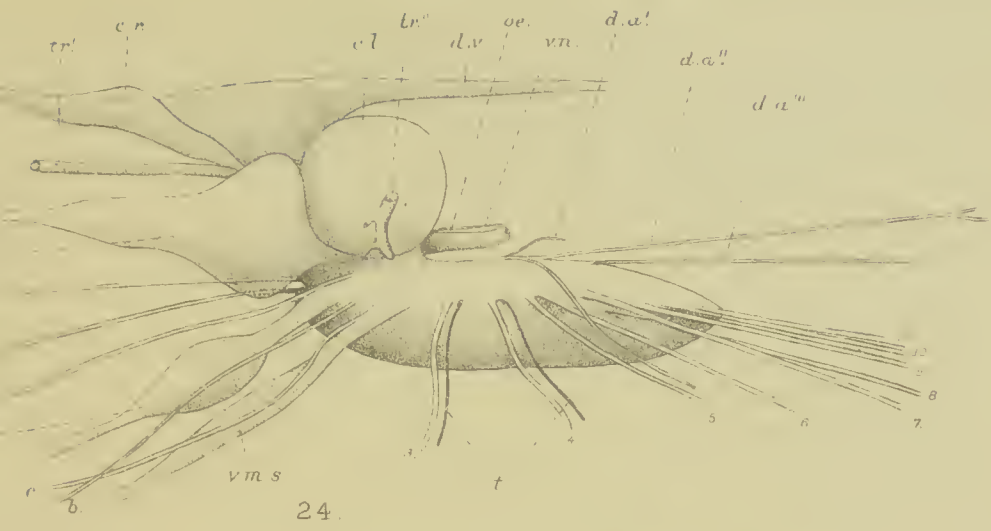


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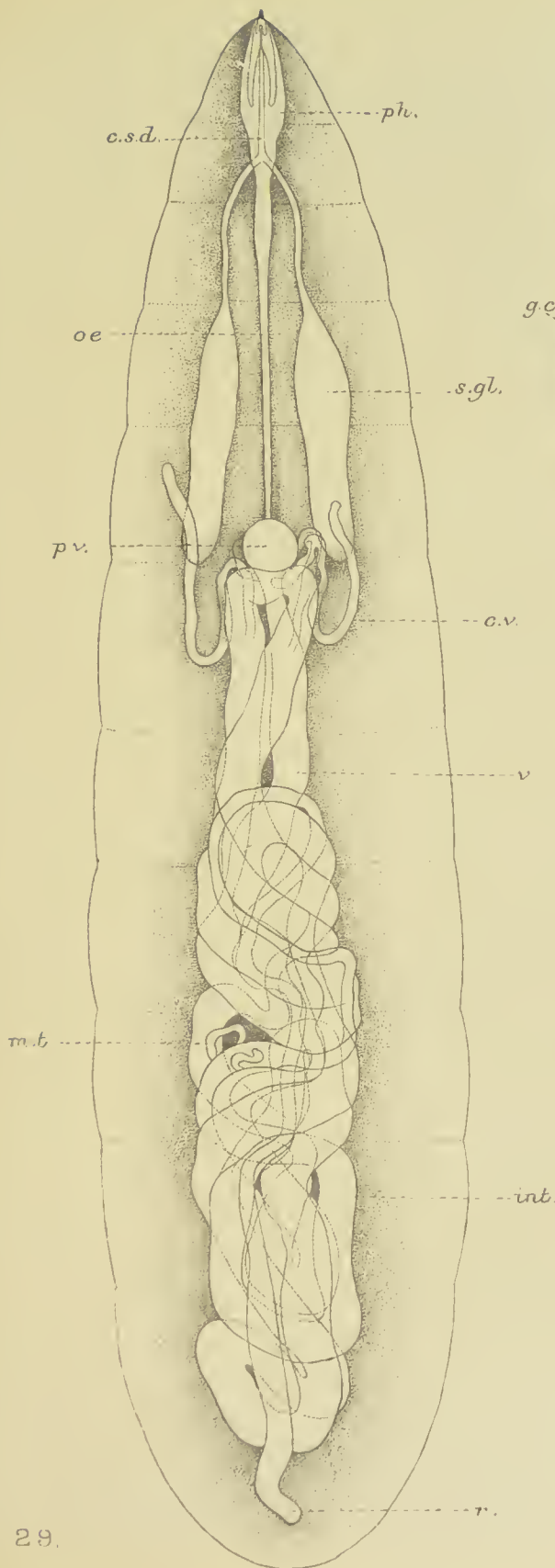


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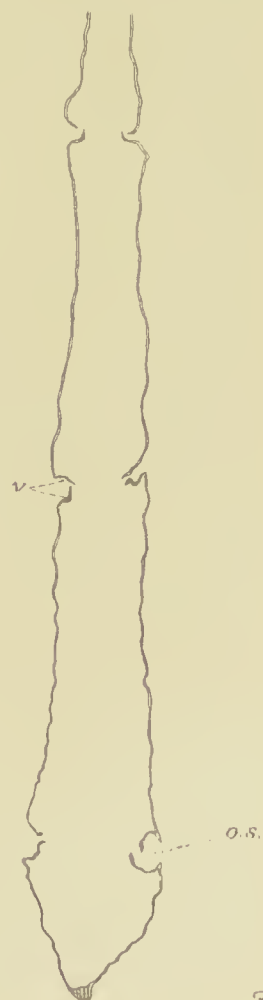




29.



30.



31.





## The Structure, Development, and Bionomics of the House-fly, *Musca domestica*, Linn.

Part III.—The Bionomics, Allies, Parasites, and the Relations  
of *M. domestica* to Human Disease.

By

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With Plate 22.

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## I. INTRODUCTION.

THE present paper concludes this study of the structure, development, and bionomics of *Musca domestica* (the previous parts were published in 1907 and 1908). In it I have described the bionomics, certain of its allies which may occur in houses, its parasites, and its relation to man, especially as the carrier of the bacilli of certain infectious diseases.

The last portion of the present paper, in which is described what is known concerning the ability of *M. domestica* and its allies to carry and disseminate the bacteria of many important diseases, shows, I hope, the grave character of its relation to man. Although its importance in this respect is being gradually realised in this country, it is not so widely recognised as it should be. In the United States of America it is proposed to change this insect's name from the house-fly to the "Typhoid fly"; notwithstanding certain objections to this name, it clearly indicates that more attention must be paid to preventive measures, that is, they must be reduced by the deprivation of suitable breeding-places. I have not discussed in the present paper the relation of house-flies to infantile or summer diarrhœa, chiefly because we are not yet certain as to the specific cause, but this disease may be included for the present under typhoid or enteric fever in so far as the relation of flies with it is concerned.

I should like to take this opportunity of thanking those medical men, whose names I mention later, for the kind manner in which they have replied to my inquiries concerning their observations on various diseases of which they have special knowledge.

## II. DISTRIBUTION.

*Musca domestica* is probably the most widely distributed insect to be found; the animal most commonly associated with man, whom it appears to have followed over the entire globe. It extends from the sub-polar regions, where Linnæus refers to its occurrence in Lapland, and Finmark as “*rara avis in Lapponia, at in Finmarchia Norwegiæ integras domos fere replet*,” to the tropics, where it occurs in enormous numbers. Referring to its abundance in a house near Pará in equatorial Brazil, Austen (1904) says: “At the mid-day meal they swarmed on the table in almost inconceivable numbers,” and other travellers in different tropical countries have related similar experiences to me, how they swarm round each piece of food as it is carried to the mouth.

In the civilised and populated regions of the world it occurs commonly, and the British Museum (Natural History) collection and my own contain specimens from the following localities. Certain of the localities have, in addition, been obtained from lists of insect faunas:

Asia.—Aden; North West Provinces (India); Calcutta; Madras; Bombay (it probably occurs over the whole of India); Ceylon; Central China; Hong-Kong; Shanghai; Straits Settlements; Japan.

Africa.—Port Said; Suez; Egypt; Somaliland; Nyassaland; Uganda; British E. Africa; Rhodesia; Transvaal; Natal; Cape Colony; Madagascar; Northern and Southern Nigeria; St. Helena; Madeira.

America.—Distributed over North America; Brazil; Monte Video (Uruguay); Argentine; Valparaiso; West Indies.

Australia and New Zealand.

Europe and the isles of the Mediterranean; it is especially common in Cyprus.

Not only is this world-wide distribution of interest, but its distribution in our own country is noteworthy. From observations that I have made during a number of years in town and

suburban houses and country houses and cottages, I find that in the former it is by far the commonest house-fly. But whereas *M. domestica* may be almost the only species in warm places where food is present, such as restaurants and kitchens, in other rooms of houses *Homalomyia canicularis*, the small house-fly, increases in proportion and often predominates; occasionally one may find it to be commoner than *M. domestica*. In country houses the proportions vary by the intrusion of *Stomoxys calcitrans*, which I have often found to be the dominant species. In a certain country cottage, out of the several hundreds captured, *S. calcitrans* formed 50 per cent. of the total, the rest being chiefly *H. canicularis* together with *Anthomyia radicum*, whose larvæ, as I have shown (1907), breed in horse-manure with those of *M. domestica*. The following records taken from a "fly census" that was made in 1907 may be taken as illustrative of the proportional abundance of the different species in different situations; although the numbers of these records are small the proportions are more obvious.

Place.	<i>M. domestica</i> .	<i>H. canicularis</i> .	Other species.
Restaurant, Manchester .	1869	14	2 ( <i>M. stabulans</i> , <i>C. erythrocephala</i> ).
Kitchen, detached suburban house (six records), Laneashire . . . .	581	265	14
Kitchen, detached suburban house in Manchester	682	7	14
Stable, suburban house .	22	153	14
Bedroom, suburban house .	1	33	(12. <i>S. calcitrans</i> ). 4 ( <i>M. stabulans</i> ).

Out of a total of 3856 flies caught in different situations, such as restaurants, kitchens, stables, bedrooms and hotels, 87·5 per cent. were *M. domestica*, 11·5 per cent. *H. canicularis*, and the rest were other species such as *S. calcitrans*, *Muscina stabulans*, *C. erythrocephala*, and *Anthomyia radicum*. These figures are comparatively small, but

are representative of the average occurrence, as I have observed, of the different species.

For the proportional occurrence in similar localities we have interesting figures given by Howard (1900) for the United States. Of 23,087 flies caught in rooms where food supplies are exposed he found that 22,808, or 98·8 per cent. of the whole number, were *M. domestica*, and of the remaining 1·2 per cent. *H. canicularis* was the commonest species. Hamer (1908) found that more than nine tenths of the flies caught in the kitchens and "living-rooms" of houses in the neighbourhood of dépôts for horse-refuse, manure, etc., were *M. domestica*. In a further report Hamer gives more details as to the different species that were found. In one lot of 35,000 flies caught on four fly-papers exposed in similar positions, 17 per cent. were *Homalomyia canicularis*, less than 1 per cent. were *C. erythrocephala*, and considerably less than 1 per cent. were *Muscina stabulans*, whereas of nearly 6000 flies caught in another situation in four fly-balloons 24 per cent. were *H. canicularis*, 15 per cent. were *C. erythrocephala*, and nearly 2 per cent. were *M. stabulans*. He gives an interesting diagram showing from counts of flies the seasonal prevalence which I have previously recorded from observation. The report shows how the proportions of the different species vary in different situations according to the substances and refuse that are present in the locality. We may therefore say with certainty that *M. domestica* is the commonest species of house-fly, and next to this *H. canicularis*, and that in country houses *S. calcitrans* often occurs in large numbers, although it is not a house-fly in the strict sense of the word.

### III. FLIES OCCURRING AS CO-INHABITANTS OF HOUSES WITH *M. DOMESTICA* OR AS VISITANTS.

We have seen from the preceding section that *M. domestica* is by far the commonest species which occurs in houses, and is, in fact, "domesticated" in the true sense of the word

—Linnaeus never selected a more truly specific title; nevertheless, other species of closely allied flies are found in houses. These may be either co-inhabitants, that is, living in houses, as in the case of *H. canicularis* and one or two others to be mentioned subsequently, or they may be visitants. The visitants normally lead an open-air life, but sometimes, as in the case of *Stomoxys calcitrans*, they spend a portion of their time in houses, when climatic conditions are less favourable for out-door life. Such flies as the blow-fly, or "blue-bottle," *Calliphora erythrocephala*, and its allies, enter houses only in search of suitable substances upon which to deposit their eggs. The appearance in houses of certain flies, as, for example, *Pollenia rudis*, can only be regarded as accidental, and the cause may be often traced to the occurrence of climbing plants such as ivy or other creepers on the walls of the house.

In India two species of flies closely allied to *M. domestica* are found—*Musca domestica* sub-sp. *determinata* Walker and *M. enteniata*, both of which, on account of their close resemblance to *M. domestica* and the similarity of their breeding habits, are frequently mistaken for it.

(1) *M. domestica* sub-sp. *determinata* Walker.

This Indian variety of the house-fly was described by Walker (1856) from the East Indies. His description is as follows: "Black, with a hoary covering; head with a white covering; frontalia broad, black, narrower towards the feelers; eyes bare; palpi and feelers black; chest with four black stripes; abdomen cinereous, with a large tawny spot on each side at the base; legs black; wings slightly grey, with a tawny tinge at the base; præbrachial vein forming a very obtuse angle at its flexure, very slightly bent inward from thence to the tip; lower cross-vein almost straight; analæ whitish, with pale yellow borders; halteres tawny."

In appearance and size it is very similar to *M. domestica*. Its breeding habits are also similar. Aldridge (1904) states



that at certain seasons of the year it is present in enormous numbers. The method of disposal of the night soil is to bury it in trenches about one foot or less in depth. From one sixth of a cubic foot of soil taken from a trench at Meerut and placed in a cage, 4042 flies were hatched. Lient. Dwyer collected 500 from one cage covering three square feet of a trench at Mhow. Specimens in the British Museum collection were obtained from the hospital kitchens, and Smith found them in a ward at Benares.

They have also been recorded from the N.W. Provinces, Kangra Valley (4500 feet), Dersa, and I have received specimens from Aden.

## (2) *Musca euteniata* Bigot.

This fly has a distribution somewhat similar to the last species, and like it, has a marked resemblance to *M. domestica*, as Bigot's (1887) description indicates :

“ Front très étroit, les yeux, toutefois, séparés. Antennis et palpes noirs ; face et joues blanches ; thorax noir avec trois larges bandes longitudinales grises ; flancs grisâtres, écusson noir avec deux bandes semblables ; cuillerons et balanciers d'un jaunâtre très pâle ; abdomen fauve, avec une bande dorsale noir et quelques reflets blancs ; pieds noirs ; ailes hyalines ; cinquième nervure longitudinal (Rondin) coudée suivant un angle légèrement arrondi, ensuite un peu concave ; deuxième transversale (l'extreme) presque perpendiculaire, légèrement bisinueuse, soudée à la cinquième longitudinale, à égale distance du conde et de la première nervure transversale (l'interne).”

*M. euteniata* measures 4 to 5 mm. in length. The British Museum collection contains specimens sent by Major F. Smith from Benares, with these notes : “ Bred from human ordure ; hospital ward fly ; at an enteric stool ; bred from cow-dung fuel cakes.” I have received specimens from Suez and Aden, and it is recorded as breeding in human excrement in Khartoum (Balfour, 1908) and in stable refuse, as also *M*

*domestica* and *M. corvina*. It will be seen, therefore, that its breeding habits are very similar to those of *M. domestica* and the sub-species *determinata*. It is interesting and important to note the rather exceptional choice of cow-dung as a breeding-place.

(3) *Homalomyia canicularis* L.

This species of fly (see 'Quart. Journ. Micr. Sci.,' vol. 51, Pl. 22, fig. 3) is often mistaken by the uninitiated for *M. domestica* which are not full grown. Although it may be called the small or lesser house-fly its differences from *M. domestica* are great, as it belongs to a different group of calypterate Muscidae, namely, the Anthomyidae. One of the chief distinguishing features of this group is that the fourth longitudinal vein of the wing (*M.* 1 + 2) goes straight to the margin of the wing and does not bend upwards at an angle as in *M. domestica*.

The male of *H. canicularis* differs from the female in some respects. In the male the eyes are close together, and the frontal region is consequently very narrow; the sides of this, these are the inner orbital regions, are silvery white, separated by a narrow black frontal stripe. In the female the space between the inner margins of the eyes is about one third of the width of the head; the frons is brownish black, and the inner orbital regions are dark ashy grey. The bristle of the antenna of *H. canicularis* is bare; in *M. domestica*, it will be remembered, the bristle bears a row of setae on its upper and lower sides. The dorsal side of the thorax of the male is blackish grey with three rather indistinct longitudinal black lines. In the female it is of a lighter grey, and the three longitudinal stripes are consequently more distinct. The abdomen of the male *H. canicularis* is narrow and tapering compared with that of *M. domestica*. It is bronze black in colour, and each of the three abdominal segments has a lateral translucent area, so that when it is seen against the light, as on a window-pane, three, and sometimes four, pairs of yellow translucent areas can be seen by the trans-

mitted light. In the female the abdomen is short in proportion to its length, and is of a greenish or brownish-grey colour.

*H. canicularis* appears in houses before *M. domestica*, and can be found generally in May and June. In the latter month its numbers are swamped, as it were, by *M. domestica*, and it appears to seek the other rooms of a house than the kitchen, although I have found it frequently in considerable numbers in kitchens. The average length is 5·7 mm.

The larva of *H. canicularis* (Pl. 22, fig. 1) is very distinct from that of *M. domestica*, as will be seen from the figure. It is compressed dorso-ventrally, and has a double row of processes on each side. Owing to the rough and spinous nature of these processes dirt adheres to the larva and gives it a dirty-brown appearance. The full-grown larva measures 5–6 mm. in length. The breeding habits of *H. canicularis* are very similar to those of *M. domestica*. The larvæ feed on waste vegetable substances and also on various excremental products, but particularly, I have found, on human excrement, for which they show a great partiality. I have frequently found excrement in privy middens to be a moving mass of the larvæ of *H. canicularis*. The larval period is from three to four weeks, and the insect spends fourteen to twenty-one days in the pupal stage.

#### (4) *Homalomyia scalaris* F.

Newstead (1907) has found this species occurring as a house-fly. It is slightly larger than, though similar in many respects to, *H. canicularis*. The larva is very similar in appearance. Newstead found the larvæ in ash-pit refuse, and bred the flies from human fæces. The larvæ have been found frequently to be the cause of intestinal myiasis.

#### (5) *Anthomyia radicum* Meigen.

This member of the Anthomyidæ has been found in houses, especially those in or near the country. The female has been illustrated already (Part I, 'Quart. Journ. Micr. Sci.,' vol. 51, Pl. 22, fig. 2). The male is darker in colour, the dorsal side

of the thorax being blackish with three black longitudinal stripes; the frontal region is very narrow; the abdomen is grey with a dark median stripe. The average length of the body is 5 mm.

In the summer they are common and may be found in the neighbourhood of manure. The eggs are laid in this substance, especially in horse-manure. The larvæ have also been found feeding on the roots of various cultivated cruciferous plants, from which the insect has derived the name "root-maggot." The eggs hatch out from eighteen to thirty-six hours after deposition. The first larval stadium lasts twenty-four hours, the second forty-eight hours, and five days later the larva changes into a pupa, the whole larval life occupying about eight days. The pupal stage lasts ten days, so that in warm weather the development may be completed in nineteen to twenty days. The full-grown larvæ measure 8 mm. in length, and may be distinguished by the tubercles surrounding the caudal extremity. In this species there are six pairs of spinous tubercles surrounding the posterior end and a seventh pair is situated on the ventral surface posterior to the anus. The tubercles of the sixth pair, counting from the dorsal side, are smaller than the rest and are bifid. The arrangement of the tubercles can be seen in fig. 2. The anterior spiracular processes (fig. 3) are yellow in colour and have thirteen lobes.

#### (6) *Stomoxys calcitrans* Linn.

The species is common, especially in the country from July to October, and during these months it may be often found in houses, although Hamer's observations (1908) appear to indicate that the presence of cowsheds, in which they occur in large numbers, does not affect their numbers in houses. I have found *S. calcitrans* in large numbers in the windows of a country house in March and April, and it may be found frequently out of doors on a sunny day in May, and throughout the ensuing summer months. It is normally an outdoor insect, but appears to seek the shelter

of houses, especially during wet weather, from which habit it has no doubt derived the popular name of "storm-fly"; it is also known as the "stable-fly." As these names may be equally applicable to certain other Diptera they should be discarded.

As I have already mentioned this species is frequently mistaken by the public for *M. domestica*, which is supposed to have adopted the biting habit, although the latter is unable to inflict the slightest prick. If examined side by side the great differences between the two will be seen readily (see Part I in 'Quart. Journ. Micr. Sci., vol. 51, Pl. 22, fig. 4). *S. calcitrans* has an awl-like proboscis for piercing and blood-sucking; this projects horizontally forward from beneath the surface of the head (fig. 4). It is slightly larger and more robust than *M. domestica*; the bristles of the antennæ bear setæ on their upper sides only. The colour is brownish with a greenish tinge; the dorsal side of the thorax has four dark longitudinal stripes, the outermost pair being interrupted. At the anterior end of the dorsal side of the thorax the median light-coloured stripe has a golden appearance, which is very distinct when the insect is seen against the light. The abdomen is broad in proportion to its length, and each of the large second and third segments has a single median and two lateral brown spots; there is also a median spot on the fourth segment.

The life-history of *S. calcitrans* has been studied by Newstead (1906), and I have been able to confirm his observations during 1907 and 1908. From fifty to seventy eggs, measuring 1 mm. in length, are laid by the female. The eggs are laid on warm, decaying vegetable refuse, especially in heaps of fermenting grass cut from lawns; I have frequently confirmed this observation of Newstead's. The eggs are also deposited on various excremental substances upon which the larvæ feed. Osborne (1896) reared them in horse-mannre; Howard (1900) states that they live in fresh horse-manure, and records their occurrence in outdoor privies in some localities; Newstead reared them in moist sheep's dung; they can also be reared in cow-dung.



The larvæ are creamy-white in colour and have a shiny, translucent appearance. They are rather similar to those of *M. domestica*, but can be distinguished by the character of the posterior spiracles. These (fig. 5 and 6) are wider apart than in *M. domestica* and are triangular in shape with rounded corners; each of the corners subtends a space in which a sinuous aperture lies. The centre of the spiracle is occupied by a circular plate of chitin. The anterior spiracular processes are five-lobed. Under warm conditions Newstead found that the egg state lasted from two to three days; the larval stage lasts from fourteen to twenty-one days and the pupal stage nine to thirteen days. There are three larval stages. The whole life-history may be complete in twenty-five to thirty-seven days. Some specimens passed the winter in the pupal state.

Although *S. calcitrans* does not frequent to such a great extent as *M. domestica* material likely to contain pathogenic intestinal bacilli, on account of its blood-sucking habits, which cause it to attack cattle and not infrequently man, it may occasionally transfer the anthrax bacillus, as many have believed, and give rise to malignant pustule, etc.

#### (7) *Calliphora erythrocephala* Mg.

This is the commoner of the two English blow-flies or "blue-bottles." The other species, *Calliphora* (*Musca*) *vomitaria*, is less common, although the name is frequently given to both species indiscriminately. They can be distinguished, however, by the fact that in *C. erythrocephala* the genæ are fulvous to golden-yellow and are beset with black hairs, whereas in *C. vomitaria* the genæ are black and the hairs are golden-red.

The appearance of *C. erythrocephala* is sufficiently well known with its bluish-black thorax and dark metallic blue abdomen. Its length varies from 7 to 13 mm. The larvæ are necrophagous. The flies deposit their eggs on any fresh or decaying meat, nor is such flesh always dead. On one occasion, when obtaining fresh material in the form of wild



rabbits upon which to rear the larvæ of *C. erythrocephala*, I found the broken leg of a live rabbit, which had been caught in a spring trap set the previous evening, a living mass of small larvæ, which were devouring the animal while it was still alive. An enormous number of eggs are laid by a single insect; Portchinski ('Osten. Sacken,' 1887) found from 450 to 600 eggs, though I have not found so many. With an average mean temperature of 23° C. (73·5° F.) and using fresh rabbits as food for the larvæ, the following were the shortest times in which I reared *C. erythrocephala*. The eggs hatched from ten to twenty hours after deposition. The larvæ underwent the first ecdysis eighteen to twenty-four hours after hatching; the second moult took place twenty-four hours later, and the third larval stage lasted six days, the whole larva life being passed in seven and a half to eight days. Fourteen days were spent in the pupal state; thus the development was complete in twenty-two to twenty-three days. I have no doubt that this time could be shortened by the presence of a very plentiful supply of food, as an enormous amount, comparatively, is consumed.

The full-grown larva may measure as much as 18 mm. in length. The posterior extremity is surrounded by six pairs of tubercles arranged as shown in the figure (fig. 12); there is also a pair of anal tubercles. The anterior spiracular (fig. 11) processes are nine-lobed. The posterior spiracles (fig. 10) are circular in shape and contain three slit-like apertures. In the second larval instar (fig. 9) there are only two slits in each of the posterior spiracles, and in the first larval instar (fig. 8) each of the posterior spiracles consists of a pair of small slit-like orifices. Howard (1900) found the fly on fresh human fæces, and Riley records it as destroying the Rocky Mountain locust.

*C. erythrocephala* is an outdoor fly, but frequently enters houses in search of material upon which to deposit its eggs and also for shelter. From its habit of frequenting fæces, which may be observed in this country especially in insanitary court-yards, and such food as meat and fruit, it is not improb-

able that it occasionally may bear intestinal bacilli on its appendages or body and thus carry infection. Its flesh-seeking habits may also render it liable to carry the bacilli of anthrax should it have access to infected flesh.

(8) *Muscina* (*Cyrtoneura*) *stabulans* Fallen.

This common species is frequently found in and near houses. I have usually found it occurring with *H. canicularis* in the early summer (June) before *M. domestica* has appeared in any numbers. It is larger than *M. domestica*, and more robust in appearance. Its length varies from 7 to nearly 10 mm. Its general appearance is grey. The head is whitish-grey with a "shot" appearance. The frontal region of the male is velvety black and narrow; that of the female is blackish-brown, and is about a third of the width of the head. The bristle of the antenna bears setæ on the upper and lower sides. The dorsal side of the thorax is grey and has four longitudinal black lines; the scutellum is grey. The abdomen, as also the thorax, is really black covered with grey; in places it is tinged with brown, which gives the abdomen a blotched appearance. The legs are rather slender, and are reddish-gold or dirty orange and black in colour.

The eggs are laid upon the following substances, on which the larvæ feed: Decaying vegetable substances such as fungi, fruit, cucumbers, decaying vegetables, and they sometimes attack growing vegetables, having been introduced probably as larvæ with the manure, as they also feed on rotting dung and cow-dung. Howard (l. c.) found the fly frequenting human excrement, and observed the species breeding in the same. In the United States it has been reared from the pupæ of the cotton-worm and the gipsy moth; Riley was of the opinion that in the first case it fed on the rotten pupæ only. In 1891 it was also reared on the masses of larvæ and pupæ of the elm-leaf beetle. Other observers record it as being reared from the pupæ of such Hymenoptera as *Lophyrus*. In all these cases of its occurrence in the pupæ of insects, it

is difficult to say whether it is parasitic or whether it feeds on the rotting pupæ only; many observers are inclined to take the last view. The larva may reach a length of 11 mm. It is creamy-white in colour; the anterior spiracular processes are five-lobed and are like hands from which the fingers have been amputated at the first joint. The posterior spiracles are rounded and enclose three triangular-shaped areas, each containing a slit-like aperture. I have not been able to study the complete life-history, but Taschenberg (l. c.) states that it occupies five or six weeks.

#### (9) *Lucilia Cæsar* L.

Although it is not a house-fly, this common fly occasionally occurs in houses, especially those in the country, and it is often called a "blue-bottle." It is smaller than *C. erythrocephala* and is more brilliant in colouring, being of a burnished gold, sometimes bluish, and also of a shining green colour.

It frequents the excrement of man and other animals in which it is able to breed. Howard (l. c.) reared it from human excrement. It also breeds in carrion, but the chief breeding-place in which I have found it in this country is on the backs of sheep. It is one of the destructive species of "maggots" of sheep. The larvæ are very similar to those of *C. erythrocephala*—in fact, Portchinski considered them indistinguishable from the larvæ of the latter except in size. The full-grown larva measures 10–11 mm. in length. The larval life lasts about fourteen days, and the pupal stage a similar length of time, but I have reason to believe that under very favourable conditions development may take place in a much shorter time.

#### (10) *Psychoda* spp.

There may be found frequently on window-panes small, grey, moth-like flies belonging to the family Psychodidæ. The wings of these small flies are large and broad in proportion to the size of the body, and are densely covered with hair; when the insect is at rest they slope in a roof-like

manner. The larvæ of some species breed in human and other excrement, others breed in decaying vegetable substances, while certain species breed in water, especially when polluted with sewage, and these aquatic species have the spiracular apparatus modified accordingly. Although a form, *Phlebotomus*, which occurs in Southern Europe, has blood-sucking habits, the British species have no such annoying habits, and are of little importance in their relation to man.

#### IV. PHYSIOLOGY.

##### 1. The Influence of Food, Temperature, and Light.

Food.—Mention has already been made in the second part of this work of the influence of food on the development of the larvæ; the experiments which were carried out showed that the larvæ develop more rapidly in certain kinds of food, such as horse-manure, than in others. It has yet to be discovered what are the chemical constituents which favour the more rapid development. It was found that insufficient food in the larval state retarded development and produced flies which were subnormal in size. Bogdanow (1908), in an interesting experiment, fed *M. domestica* through ten generations on unaccustomed food such as meat and tanacetum in different proportions, and he found that the resulting flies did not show any change.

Temperature.—The influence of temperature on the development of the larvæ has been shown also. A high temperature accelerates the development of the egg, larva and pupa. Temperature also affects the adult insect; they are most active at a high summer temperature, and cold produces an inactive and torpid condition. They are able, however, to withstand a comparatively low temperature. Bachmetjew (1906) was able to submit *M. domestica* to as low a temperature as  $-10^{\circ}\text{C}$ ., and vitality was retained, as they recovered when brought into ordinary room temperature. Donhoff (1872) performed a number of experiments previous

to this with interesting results. He submitted *M. domestica* for five hours to a temperature of  $-1.5^{\circ}\text{C.}$ , and they continued to move. Exposed for eight hours to a temperature of first  $-3^{\circ}\text{C.}$  and then  $-2^{\circ}\text{C.}$  they moved their legs. On being submitted for twelve hours to a temperature first of  $-3.7^{\circ}\text{C.}$  and then  $-6.3^{\circ}\text{C.}$ , they appeared to be dead, but on being warmed they recovered. When exposed for three hours to a temperature of  $-10^{\circ}\text{C.}$  which was then raised to  $-6^{\circ}\text{C.}$ , they died. These experiments show that *M. domestica* is able to withstand a comparatively low degree of temperature.

Light.—The female of *M. domestica* deposits the eggs in dark crevices of the substance chosen for the larval nidus and as far away from the light as possible. Béclard (1858) showed that the eggs develop more quickly under blue and violet glass than under red, yellow, green, or white. The larvæ are negatively heliotropic, as Loeb (1890) has also proved in the larvæ of the blow-fly. As I have previously shown, the distinction between light and darkness is probably appreciated by the larvæ by means of the sensory tubercles of the oral lobes.

## 2. Hibernation.

This question is intimately connected with the preceding physiological facts. The disappearance of the flies towards the end of October and in November is a well-known fact, and an endeavour to discover the reason for this has been made in the present investigation.

I have found that the majority of flies observed were killed off by the fungus *Empusa muscæ* Cohn which is described in the present paper. Of the remainder some hibernate and some die naturally. This natural death may be compared, I think, to the like phenomenon that occurs in the case of the hive-bee *Apis mellifica*, where many of the workers die at the end of the season by reason of the fact that they are simply worn out, their function having been fulfilled. The flies which die naturally have probably lived for many



weeks or months during the summer and autumn, and in the case of the females have deposited many batches of eggs; their life work, therefore, is complete. Those flies which hibernate are, I believe, the most recently emerged, and therefore the youngest and most vigorous. On dissection it is found that the abdomens of these hibernating individuals are packed with fat cells, the fat body having developed enormously. The alimentary canal shrinks correspondingly and occupies a very small space; this is rendered possible by the fact that the fly does not take food during this period. In some females it was found that the ovaries were very well developed, while in others they were small, and mature spermatozoa were found in the males. Like most animals in hibernating, *M. domestica* becomes negatively heliotropic and creeps away into a dark place. In houses they have been found in various kinds of crevices such as occur between the woodwork and the walls. A favourite place for hibernation is between wall-paper which is slightly loose and the wall. A certain number hibernate in stables, where, owing to the warmth, they do not become so inactive, and they emerge earlier at the latter end of spring. During the winter the hibernating flies are sustained by means of the contents of the fat body, which is found to be extremely small in hibernating flies if dissected when they first emerge in May and June. The abdominal cavity is at first considerably decreased in size, but the fly begins to feed and soon the alimentary tract regains its normal size, and, together with the development of the reproductive organs, causes the abdomen to regain its normal appearance. The emergence from hibernation appears to be controlled by temperature, as one may frequently find odd flies emerging from their winter quarters on exceptionally warm days in the early months of the year (see Appendix).

### 3. Flight.

The distance that *M. domestica* is able to fly is one of practical importance in connection with their breeding habits



and disease-germ-carrying powers. Normally they do not fly great distances. They may be compared to domestic pigeons which hover about a house and the immediate neighbourhood. On sunny days they may be found in large numbers out-of-doors, but they retire into the houses when it becomes dull or rains. They are able to fly, however, a considerable distance, and can be carried by the wind. A few years ago, when visiting the Channel Islands, I found *M. domestica* from  $1\frac{1}{2}$  to 2 miles from any house or any likely breeding-place, so far as I was able to discover. Dr. M. B. Arnold has made some exact experiments at the Monsall Fever Hospital, Manchester, on the distance travelled by flies.<sup>1</sup> Three hundred flies were captured alive, and marked with a spot of white enamel on the back of the thorax. These were liberated in fine weather. Out of the 300 five were recovered in fly-traps at distances varying from 30 to 190 yards from the place of liberation, and all the recoveries were within five days. *M. domestica* is also able to fly at a considerable height above ground, and I have found them flying at an altitude of 80 feet above the ground. Such a height would greatly facilitate their carriage by the wind.

#### 4. Regeneration of Lost Parts.

If the wings or legs of *M. domestica* are broken off they do not appear to be able to regenerate the missing portions, as in the case of some insects, notably certain Orthoptera. Kammerer (1908), however, experimenting with *M. domestica* and *C. vomitoria*, has found that if the wing is extirpated from a recently pupated fly it is occasionally regenerated. The new wing is at first homogeneous, and contains no veins, but these appear subsequently.

<sup>1</sup> Recorded on p. 262 of the 'Report on the Health of the City of Manchester for 1906,' by James Niven, 1907.

## V. NATURAL ENEMIES AND OCCASIONAL PARASITES.

The most important of all the natural enemies of *M. domestica* is the parasitic fungus *Empusa museæ*, which will be described here; this is the most potent of the natural means of destruction. Of animals, apart from the higher animals such as birds, spiders probably account for the greatest number, though owing to the normally clean condition of the modern house these enemies of the house-fly are refused admittance. I have been unable to rear any insect parasites, such as ichneumons, from *M. domestica*. Their life indoors and the cryptic habits of the larvæ no doubt save them from the attacks of such insects; but Packard (1874) records the occurrence of the pupa of what was probably a Dermestid beetle, which he figures; this was found in a pupa of *M. domestica*. Predatory beetles and their larvæ probably destroy the larvæ, and Berg (1898) states that a species of beetle, *Trox suberosus* F., known as "Champi" in S. America, is an indirect destructor of the common fly. I have frequently observed the common wasp, *Vespa germanica*, seize *M. domestica* and carry it away. In some places in India it is the custom, so I have been told by residents, to employ a species of Mantis, one of the predatory "praying insects," to destroy the house-flies.

In view of the fact that the Arachnids *Chernes nodosus* and the species of Gamasid are occasionally found actually attached in a firm manner to *M. domestica*, they will be described under this head, but it must be clearly understood that it is still an open question whether they are external parasites in the true sense of the word, or whether *M. domestica*, instead of being the host, is merely the transporting agent as it appears to be in the majority of cases. For the present they may be termed for convenience "occasional parasites," in view of the fact that they have been found occasionally feeding upon *M. domestica*.

1. *Chernes nodosus* Schrank.

There are frequently found attached to the legs of the house-fly small scorpion or lobster-like creatures which are Arachnids belonging to the order Pseudo-scorpionidea; the term "chelifers" is also applied to them on account of the large pair of chelate appendages which they bear. The species which is usually found attached to *M. domestica* is *Chernes nodosus* Schrank (fig. 13). It is very widely distributed, and my observations agree with those of Pickard-Cambridge (1892), who has described the group.

The species is 2.5 mm. in length and Pickard-Cambridge's description of it is as follows:

"Cephalothorax and palpi yellowish red-brown, the former rather duller than the latter. Abdominal segments yellow-brown; legs paler. The caput and first segment of the thorax are of equal width (from back to front); the second segment of the thorax is very narrow. The surface of the cephalothorax and abdominal segments is very finely shagreened, the latter granulose on the sides. The hairs on this part as well as on the palpi and abdomen are simple, but obtuse. The palpi are rather short and strong. The axillary joint is considerably and somewhat subconically protuberant above as well as protuberant near its base underneath. The humeral joint at its widest part, behind, is considerably less broad than long; the cubital joint is very tumid on its inner side; the bulb of the pincers is distinctly longer, to the base of the fixed claw, than its width behind; and the claws are slightly curved and equal to the bulb in length."

They appear to be commoner in some years than in others. Godfrey (1909) says: "The ordinary habitat of *Ch. nodosus*, as Mr. Wallis Kew has pointed out to me, appears to be among refuse, that is, accumulations of decaying vegetation, manure-heaps, frames and hot-beds in gardens. He refers to its occurrence in a manure-heap in the open air at Lille, and draws my attention to its abundance in a melon-frame near Hastings in 1898, where it was found by Mr. W. R. Butterfield." In

view of these facts it is not difficult to understand its frequent occurrence on the legs of flies, which may have been on the rubbish heaps either for the purpose of laying eggs, or, what is more likely, because they have recently emerged from pupæ in those places and in crawling about, during the process of drying their wings, etc., their legs were seized by the *C. nodosus*.

The inter-relation of the *Chernes* and *M. domestica*, however, is one of no little complexity; much has been written and many diverse views are held concerning it. An interesting historical account of the occurrences of these Arachnids on various insects has been given by Kew (1901). Three views are held in explanation of the association and they are briefly these: First, that the *Chernes*, by clinging passively to the fly, uses it as a means of transmission and distribution; second, that the Arachnid is predaceous; and third, that it is parasitic on the fly. Owing to the unfortunate absence of convincing experimental proof in favour of either of the last two opinions, it is practically impossible to give any definite opinion as to the validity of these views; nevertheless they are worthy of examination.

The dispersal theory was held by Pickard-Cambridge and Moniez (1894). Whether the other views are held or not there is no doubt that such an association, even if it were only accidental, would result in a wider distribution of the species of *Chernes*, as the flies are constantly visiting fresh places suitable as a habitat for the same. Except in one or two recorded cases the Arachnids are always attached to the legs of the fly, the chitin of which is hard and could not be pierced, a fact which is held in support of this theory as the only explanation of the association.

The parasitic and predaceous views are closely related. The *Pseudo-scorpionidea* feed upon small insects, which they seize with their chelæ. It is suggested by some that the *Chernes* seizes the legs of the fly without realising the size of the latter. Notwithstanding its size, however, they remain attached until the fly dies and then feed upon the

body. In some cases as many as ten of the Arachnids have been found on a single fly, and if the movements of the insect are impeded by the presence of a number of the Chernes it will be easily understood that the life of the fly will be curtailed thereby. Pseudo-scorpionidea have been observed feeding on the mites that infest certain species of Coleoptera, and it has been suggested that they associated with the flies for the same purpose, although I do not know of any recorded case of a fly infested with mites carrying Chernes also. If this were the case the Chernes would be a friend and not a foe of the fly, as Hickson (1905) has pointed out.

There are few records to support the view that the Chernes is parasitic on the fly. Donovan (1797) mentions the occurrence of a pseudo-scorpionid on the body of a blow-fly, and Kirby and Spence (1826) refer to their being occasionally parasitic on flies, especially the blow-fly, under the wings of which they fix themselves. It is probable that the Chernes seldom reaches such a position of comparative security on the thorax of the fly; should it succeed in doing so, however, it could become parasitic in the true sense of the word. As I have previously pointed out, little experimental evidence is at present available and further investigation is necessary before it is possible to maintain more than a tentative opinion with regard to this association between the Chernes and the fly. It is obvious that the association will result in the distribution of the Pseudo-scorpionid, but whether this is merely incidental and the real meaning lies in a parasitic or predaceous intention on the part of the Arachnid, as some of the observations appear to indicate, further experiments alone will show.

## 2. Acarina or Mites borne by House-flies.

As early as 1735 de Geer observed small reddish Acari in large numbers on the head and neck of *M. domestica*. They ran about actively when touched. The body of this mite was oval in shape, completely chitinated, and polished;



the dorsal side was convex and the ventral side flat. Linnæus (1758) called this mite *Aearus muscarum* from de Geer's description, and Geoffroy (1764) found what appears to be the same, or an allied species of, mite, which he called the "brown fly-mite." Murray (1877) describes a form, *Trombidium parasiticum*,<sup>1</sup> which is a minute blood-red mite parasitic on the house-fly. He says: "In this country they do not seem so prevalent, but Mr. Riley mentions that in North America, in some seasons, scarcely a fly can be caught that is not infested with a number of them clinging tenaciously round the base of the wings." As it only possessed six legs it was doubtless a larval form.

Anyone who has collected Diptera as they have emerged from such breeding-places as hot-beds, rubbish and manure heaps will have noticed the frequently large number of these insects which are to be found carrying immature forms of the Acari. These are being transported merely by the flies in the majority of cases. Mr. Michael tells me that he used to call such flies "the emigrant waggons"—a very descriptive term. Many of these mites belong to the group Gamasidæ—the super-family Gamasoidea of Banks (1905). These mites have usually a hard coriaceous integument. In shape they are flat and broad and have rather stout legs. Sometimes immature forms of these mites swarm on flies emerging from rubbish heaps. Banks holds the opinion that they are not parasitic, but that the insect is only used as a means of transportation. It is difficult to decide whether this is so in all cases. I have illustrated (fig. 14) a specimen of the small house-fly, *H. canicularis*, caught in a room; on the under-side of the fly's abdomen a number of immature Gamasids<sup>2</sup> are attached,

<sup>1</sup> This species was named *Atoma parasiticum* and later *Astoma parasiticum* by Latreille ('Magazin Encyclopedique,' vol. iv, p. 15, 1795). Mr. A. D. Michael tells me that the genus was founded on *Trombidium parasiticum* of de Geer. They were really larval Trombididæ and *Atoma* was founded on larval characters; probably any larval *Trombidium* came under the specific name.

<sup>2</sup> Being unable to identify these immature specimens I submitted them to Mr. Michael, who kindly informs me that it is extremely diffi-



apparently by their stomal regions. These specimens may be truly parasitic, as I am inclined to believe, since many *Acari* are parasitic in the immature state, although the adults may not be so; on the other hand this form of attachment may be employed as a means of maintaining a more secure hold of the transporting insect.

### 3. Fungal Disease—*Empusa muscæ* Cohn.

Towards the end of the summer large numbers of flies may be found attached in a rigid condition to the ceiling, walls or window-panes. They have an extremely life-like appearance, and it is not until one examines them closely or has touched them that their inanimate, so far as the life of the fly is concerned, condition is discovered. These flies have been killed by the fungus *Empusa muscæ* Cohn, and in the later stages of the disease its fungal nature is recognised by the fact that a white ring of fungal spores may be seen around the fly on the substratum to which it is attached. The abdomen of the fly is swollen considerably, and white masses of sporogenous fungal hyphæ may be seen projecting for a short distance from the body of the fly, between the segments, giving the abdomen a transversely striped black and white appearance.

The majority of flies which die in the late autumn—and it is then that most of the flies which have been present during the summer months perish—are killed by this fungus. Its occurrence, therefore, is of no little economic value, especially if it were possible to artificially cultivate it and destroy the flies in the early summer instead of being compelled to wait until the autumn for the natural course of events.

*Empusa muscæ* belongs to the group *Entomophthorææ*, the members of which confine their attacks to insects, and in many cases, as in the case of the present species, are productive of great mortality among the individuals of the species of

cult to identify immature *Gamasids* owing to the scarcity of knowledge as to their life-histories, but he says that they are very like *Dinychella asperata* Berl.

insect attacked. In this country it may be found from about the beginning of July to the end of October, and usually occurs indoors. It appears to be very uncommon out-of-doors. A case has been recently recorded<sup>1</sup> of its occurrence on Esher Common, where it had attacked a species of Syrphid, *Melanostomum scalare* Fabr. Thaxter (1888) also mentions two cases of its occurrence out-of-doors in America, in both of which cases it had attacked, singularly enough, species of Syrphidæ. This author states that *Empusa muscæ* is probably the only species which occurs in flowers attractive to insects, but he only observed it on the flowers of *Solidago* and certain Umbellifereæ.

The development of this species was studied by Brefeld (1871). An *Empusa* spore which has fallen on a fly rests among the hairs covering the insect's body and there adheres. A small germinating hypha develops, which pierces the chitin, and after entering the body of the victim penetrates the fat-body. In this situation, which remains the chief centre of development, it gives rise to small spherical structures which germinate in the same manner as yeast cells, forming gemmæ. These separate as they are formed, and falling into the blood sinus are carried throughout the whole of the body of the fly. It was probably these bodies that Cohn (1855) found, and he explained their presence as being due to spontaneous generation; he believed that the fly first became diseased and that the fungus followed in consequence. After a period of two or three days the fly's body will be found to be completely penetrated by the fungus, which destroys all the internal tissues and organs. The whole body is filled with the gemmæ, which germinate and produce ramifying hyphæ (fig. 15). The latter pierce the softer portions of the body-wall between the segments and produce the short, stout conidiophores (*c.*), which are closely packed together in a palisade-like mass to form a compact white cushion of conidiophores, which is the transverse white ring that one finds between each of the segments of a diseased, and

<sup>1</sup> 'Trans. Ent. Soc. London,' 1908 ("Proceedings," p. 57).

consequently deceased, fly. A conidium now develops (fig. 16) by the constriction of the apical region of the conidiophore. When it is ripe the conidium (fig. 17) is usually bell-shaped, measuring  $25-30\ \mu$  in length; it generally contains a single oil-globule (*o.g.*). In a remarkable manner it is now shot off from the conidiophore, often for a distance of about a centimetre, and in this way the ring or halo of white spores, which are seen around the dead fly, are formed. In some cases, although I find that it is not an invariable rule as some would suggest, the fly, when dead, is attached by its extended proboscis to the substratum. Giard (1879) found that blow-flies killed by *Entomophthora calliphora* were attached by the posterior end of the body. If the conidia, having been shot off, do not encounter another fly, they have the power of producing a small conidiophore, upon which another conidium is in turn developed and discharged. If this is unsuccessful in reaching a fly a third conidium may be produced, and so on. By this peculiar arrangement the conidia may eventually travel some distance, and it is no doubt a great factor in the wide distribution of the fungus, once it occurs. On the fly itself short conidiophores may be found producing secondary conidia.

Reproduction by conidia appears to be the only form of generation, as we are still uncertain as to the occurrence of a resting-spore stage in this species. Winter (1881) states that he found resting-spores in specimens of *M. domestica* occurring indoors; they also produced conidia which he identified as *E. muscæ*. These azygospores measured  $30-50\ \mu$  in diameter, and were produced laterally or terminally from hyphæ within the infected fly. Giard (*l. c.*) describes resting spores which were produced externally and on specimens found in cool situations. Brefeld, however, is of the opinion that *E. muscæ* does not produce resting-spores. The question of the production of resting-spores needs further investigation, as it is one of some importance. In the absence of confirmatory evidence it is extremely difficult to understand how the gap in the history of the *Empusa*, between the

late autumn of one year and the summer of the next, is filled. A number of suggestions have been made, many of which cannot be accepted; for example, Brefeld believes that the *Empusa* is continued over the winter in warmer regions, migrating northwards with the flies on the return of summer! In the case of *Entomophthora calliphora*, Giard believes that the cycle is completed by the corpses of the blow-flies falling to the ground, when the spores might germinate in the spring and give rise to conidia which infect the larvæ. Olive (1906) studied the species of *Empusa* which attacks a species of *Sciara* (Diptera) and found the larvæ infected. He accordingly thinks that the disease may be carried over the winter by those individuals which breed during that period in stables and other favourable places. As I have shown, *M. domestica*, under such favourable conditions as warmth and supply of suitable larval food, is able to breed during the winter months, although it is not a normal occurrence so far as I have been able to discover. If, then, these winter-produced larvæ could become infected they might assist in carrying over the fungus from one year to the next, and thus carry on the infection to the early summer broods of flies. This suggestion and the possible occurrence of a resting-spore stage appears to me to be the probable means by which the disease may be carried over from one "fly-season" to the next.

*E. muscæ*, besides occurring in *M. domestica*, has been found on several species of *Syrphidæ*, upon which it usually occurs out-of-doors, as I have already mentioned. In addition to these Thaxter records its occurrence in *Lucilia cæsar* and *Calliphora vomitoria*.

## VI. TRUE PARASITES.

### 1. Flagellata. *Herpetomonas muscæ-domestica* Burnett.

This flagellate has been known as a parasite of the alimentary tract of *M. domestica* for many years. Stein (1878) figures a flagellate which he calls *Cercomonas muscæ-domestica*, and identifies it with the *Bodo muscæ-*

domesticæ described by Burnett and the *Cercomonas muscarum* of Leidy. For this form figured by Stein, a new genus, *Herpetomonas*, was instituted by Kent (1880-81), and it is taken as the type-species. It was not until the economic importance of certain of the hæmo-flagellates was recognised that other flagellates, including *H. muscæ-domesticæ*, received further attention, and then Prowazek (1904) described with great detail the development of this species. In the previous year Léger (1903) had given a short account of it, and since Prowazek's memoir Patton (1908, 1909) has given short preliminary accounts of his study of the life-history. The accounts of both these authors differ in several respects from that of Prowazek, as will be shown. I have examined a very large number of the contents of English specimens of *M. domestica*, but, with one or two doubtful exceptions, unfortunately I have been unable so far to discover any of these flagellates in my film preparations.

The full-grown flagellate (VIII) measures 30-50  $\mu$  in length. The body is flattened and lancet-shaped, the posterior end being pointed and the anterior end bluntly rounded. The alveolar endoplasm contains two nuclear structures. In the centre is the large "trophonucleus" (*tr.*); it contains granules of chromatin, but is sometimes difficult to see. Near the anterior end the deeply staining rod-shaped "kinetonucleus" (blepharoplast of many authors) (*k.*) lies, usually in a transverse position. The single stout flagellum, which is a little longer than the body of the flagellate, arises from the anterior end, near the kinetonucleus. Prowazek describes the flagellum as being of a double nature and having a double origin; this, which is a mistaken interpretation, is repeated by Lingard and Jennings (1906).

This mistake, as pointed out by Léger and Patton, is due to the fact that the majority of the adult flagellates have the appearance of a double flagellum, which represents the beginning of the longitudinal division of the flagellate (VI). Patton (1908) figures a stage in *H. lygæi* with the double flagellum, and Léger (1902) in a similar stage in *H. jaculum*,



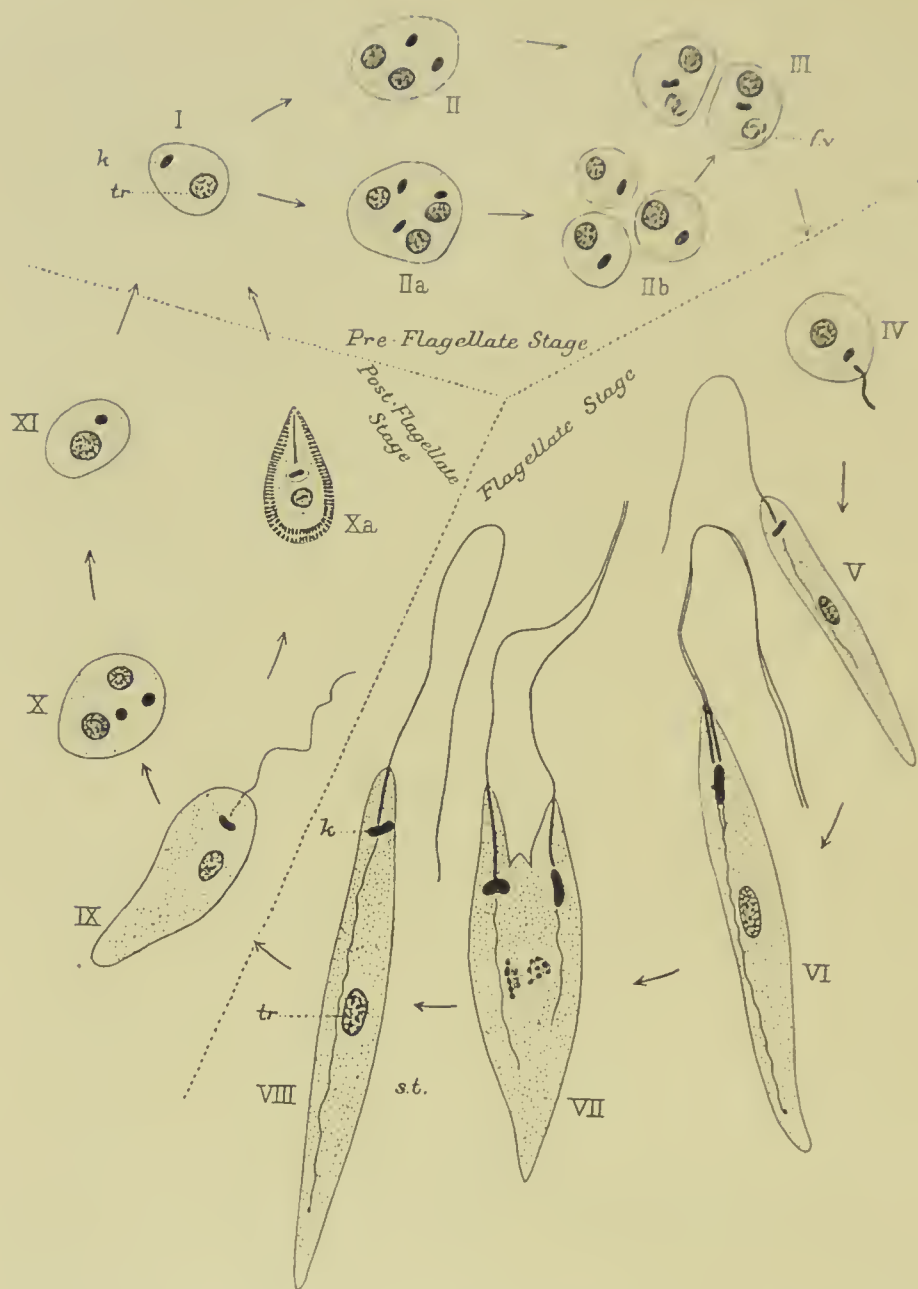


Diagram of the life-cycle of *Herpetomonas muscae-domesticae* Burnett. Arrangement chiefly after Patton; figures after Léger, Patton, and Prowazek. I-III. Preflagellate stage. IV-VIII. Flagellate stage: V. Young flagellate. VI. Flagellate beginning to divide, flagellum having already divided. VII. Advanced stage of division. VIII. Adult flagellate. IX-XI. Post-flagellate stage: IX. Degeneration of flagellum. Xa. Post-flagellate stage completed by formation of gelatinous covering, containing double row of granular bodies (Prowazek). f.v. Flagellar vacuole. k. Kinetoneucleus. s.t. Spiral chromophilous thread. tr. Trophonucleus.



parasitic in the gut of *Nepa cinerea*, from which figures it may be understood how the mistake has arisen. Through this misinterpretation Prowazek was led to consider that the parasite was of a bipolar type, in which the body had been doubled on itself so that the two ends came together and the flagellum remained distinct. The flagellum, according to Léger, is continued into the cytoplasm as a thin thread, which stains with difficulty, and terminates in a double granule above the kinetonucleus; this double granule is no doubt the "diplosome" of Prowazek. According to the latter author another deeply staining double thread (*s.t.*), that appears to be spirally coiled, runs backwards from the kinetonucleus and terminates posteriorly in a distinct granule, shown in fig. VIII.

The flagellates congregate in the proventriculus or in the posterior region of the intestine, where they become united by their anterior ends to form rosettes. Prowazek states that in the rosette condition the living portion of the flagellate resides, as it were, in the long tail-like process.

Patton divides the life-cycle of *H. muscæ-domesticæ* into three stages—the preflagellate, flagellate, and post-flagellate. The last two are common, but the first stage is not common, and Prowazek appears to have overlooked it. For convenience I have described the flagellate stage first, and the process of division in this stage is simple longitudinal fusion. The nuclei divide independently, and the kinetonucleus usually precedes the trophonucleus. The latter undergoes a primitive type of mitosis, in which Prowazek recognised eight chromosomes (VII). The flagellum divides longitudinally, and each of the two halves of the kinetonucleus appropriates one of the halves with its basal granule.

The preflagellate stage, which Patton (1909) describes, usually occurs in the masses which lie within the peritrophic membrane.<sup>1</sup> They are round or slightly oval bodies (I), their average breadth being  $5.5 \mu$ . The protoplasm is granular and

<sup>1</sup> I assume that Patton refers to this membrane by the term "peritricheal membrane."

contains a trophonucleus and kinetonucleus. Division takes place by simple longitudinal division or multiple segmentation, and in this manner a large number of individuals are formed (II *b* and III). These develop into the flagellate stage: a vacuole, the flagellar vacuole (III, *f.v.*) appears between the kinetonucleus and the rounded end of the pre-flagellate form, and in it the flagellum appears as a single coiled thread, which is extended when the vacuole has approached the surface.

The flagellate form has already been described, and in the concluding portion of the flagellate stage, which, according to Prowazek, is found in starved flies, these forms are found collecting in the rectal region, and attaching themselves by their flagellar ends in rows to gut epithelium. The more external ones begin to shorten, during which process the flagella degenerate (IX) and are shed. Thus a palisade of parasites is formed, the outer ones being rounded and devoid of flagella, and some of them may be found dividing (X). Léger (1902) terms these the "formes grégariennes," and maintains that the existence of these "gregarine" forms is a powerful argument in favour of the flagellate origin of the Sporozoa, which he had previously suggested, and which Bütschli had put forward in 1884. After the degeneration of the flagellum a thickened gelatinous covering is formed, containing a double row of granular bodies (Xa), and these cysts are regarded by Patten as the post-flagellate stage. They pass out with the faeces, and dropping on the moist window-pane or on food, are taken up by the proboscides of other flies.

Prowazek describes dimorphic forms of the flagellate stage, which he regards as sexually differentiated forms, but Patton, in a letter to me, says that he is unable to find any of these complicated sexual stages. According to Prowazek, one of these forms is slightly larger than the other, and has a greater affinity for stain. The dimorphic forms conjugate; their cell substance and nuclei fuse, and a resting-stage cyst is formed, but the subsequent stages have not been followed. He further states that the sexually differentiated forms may force

their way into the ovaries, where they undergo autogamy and infect the subsequent brood.

In Madras Patton found that 100 per cent. of the flies were infected with the flagellate; Prowazek found it in 8 per cent. of the flies at Rovigno. In the cold season in the plains (India) Lingard and Jennings (l.c.) found the flagellate in less than 1 per cent. of the flies examined; in the hills (Himalayas), at an elevation of 7500 feet, the flagellates were most numerous during the hottest season of the year, and gradually decreased in number to October and November, when none were discovered.

One of the chief points of interest in connection with this flagellate is its similarity to the "Leishmann-Donovan" body, the parasite of kala-azar, as it was this resemblance that prompted Rogers (1905) to suggest that the latter parasite was a *Herpetomonas*, which I think Patton has now conclusively proved to be the case, and he calls it *Herpetomonas donovani* (Laveran and Mesnil).

#### *Crithidia Muscæ-domesticæ* Werner.

This parasite has been recently described by Werner (1908), who found it in the alimentary tracts of four out of eighty-two flies. It measures 10–13  $\mu$  in length, the length of the body being 5–7  $\mu$  and the flagellum 5–6  $\mu$ . As in other members of the genus *Crithidia*, which is closely allied to *Herpetomonas*, the breadth of the body is great compared with the length, and the kinetonucleus and trophonucleus are rather close together. A short, staining, rod-like body lies between the kinetonucleus and the base of the flagellum. The flagellum is single. Dividing forms undergoing longitudinal division were frequently found. The kinetonucleus appears to divide first, followed in succession by the flagellum and the trophonucleus. Forms undergoing division and showing a single trophonucleus and double kinetonucleus and flagellum were also found. Cases occurred in which the fission began at the

non-flagellate end of the body. No conjugating forms were found, nor any wandering into the ovaries.

Lingard and Jennings (l. c.) describe certain flagellates of a flag-shaped or rhomboidal nature, which I am strongly of the opinion are species of *Crithidia* and not species of *Herpetomonas*. Closely following Prowazek's account of *H. muscæ-domesticæ* they describe and figure all their forms as having two flagellæ in the flagellate stage. If one allows for the rupture of the flagellum from the bodies of the organism in making the film, some of their figures are not unlike those of *Crithidia gerridis*, parasitic in the alimentary tract of an Indian water-bug, *Gerris fossarum* Fabr., and described by Patton (1908).

## 2. Nematoda—*Habronema muscæ* (Carter).

Carter (1861) appears to be the first to have described a parasitic worm in *M. domestica*. He described a bisexual nematode infesting this insect in Bombay, and found that: "Every third fly contains from two to twenty or more of these worms, which are chiefly congregated in, and confined to, the proboscis, though occasionally found among the soft tissues of the head and posterior part of the abdomen." His description of this nematode, to which he gave the name *Filaria muscæ*, is as follows: "Linear, cylindrical, faintly striated transversely, gradually diminishing towards the head, which is obtuse and furnished with four papillæ at a little distance from the mouth, two above and two below; diminishing also towards the tail, which is short and terminated by a dilated round extremity covered with short spines. Mouth in the centre of the anterior extremity. Anal orifice at the root of the tail." He gives the length as being one eleventh of an inch and the breadth as one three hundred and thirteenth of an inch. In his description of his figures of the worm he calls what is evidently the anterior region of the intestine the "liver." Von Linstow (1875) described a small nematode, which he calls *Filaria stomoxeos*, from the

head of *S. calcitrans*; this larva measured 1·6 to 2 mm. in length. Generali (1886) described a nematode from the common fly, which he calls *Nematodum spec.* It is highly probable, as my friend Dr. A. E. Shipley has suggested to me, that Generali's nematode and the *F. muscæ* of Carter are identical. Diesing (1861) created the genus *Habronema* for the *Filaria muscæ* of Carter, and his description is practically a translation of Carter's original description. Piana (1896) describes a nematode from the proboscis of *M. domestica*, which, in the occurrence of the male and female genital organs in the same individual, he says, resembles Carter's nematode. He finds that at certain seasons of the year and in certain localities it is very rare, while at others it may occur in 20–30 per cent. of the flies. The larva, after fixation, measured 2·68 mm. in length and 0·08 mm. in breadth. It was cylindrical and gently tapering off at the extremities, with the mouth terminal.

Out of the many hundreds of flies which I have dissected I have only found two specimens of this nematode (fig. 18). From the descriptions given by Carter and Piana and the figures of the latter I feel convinced that their specimens and mine are the same species, called by Diesing *Habronema muscæ* (Carter). It is linear, cylindrical, tapering gradually towards both ends. The anterior end is slightly rounded, having the mouth in the centre. I am unable to confirm the presence of the four papillæ which Carter describes as a little distance from the mouth, nor are they figured by Piana. The cuticle is very faintly marked with transverse striations. The common genital and anal orifice is situated at a short distance from the posterior end of the body, which tapers off slightly more than the anterior end and terminates in a small dilated extremity, which is covered with minute spines (fig. 19). My specimens appear to be immature adult forms, not having reached sexual maturity. The species measures 2 mm. in length and 0·04 mm. in breadth. The specimens that I obtained were situated in the head region, between the optic ganglia and the cephalic air-sacs, from which position they



could easily move down into the cavity of the proboscis. I am unaware of any previous record of the occurrence of *Habronema muscæ* in this country, but I have no doubt that if one searched specially for it it would be found to occur more commonly than might appear from my experience, and to be generally distributed with its host throughout the world.

The occurrence of a parasitic worm in this position is of great interest, even though *M. domestica* is not a blood-sucking species and the nematode is not of the nature of *Filaria bancrofti*. There is no reason, however, why *M. domestica* should not under certain conditions carry pathogenic nematodes, which might easily get on to the food of man.

### 3. Dissemination of Parasitic Worms.

In this connection reference might be made to the experiments of Grassi (1883) to which reference is made by Nuttall in his valuable memoir (1899). Grassi broke up segments of *Tænia solium* in water; they had previously been preserved in alcohol for some time. Flies sucked up the eggs in the water and he found them unaltered in the fæces. *Oxyuris* eggs were also passed unaltered. In another experiment flies fed on the eggs of *Trichocephalus* and he found the eggs some hours afterwards in the flies' fæces, which had been deposited in the story beneath the laboratory; he also caught flies in this kitchen with their intestines full of eggs.

Calandruccio<sup>1</sup> examined flies (? species) which had settled upon fæces containing the ova of *Tænia nana*. The ova were found in the flies' intestines. The excrement deposited by a fly on sugar contained two or three ova of the *Tænia*. By means of such infected sugar a girl was infected, and ova of *T. nana* were found in her stools on the twenty-seventh day.

<sup>1</sup> "Ulteriori ricerche sulla *Tænia nana*." 'Boll. Soc. Zool. Ital. Roma,' vol. vii, pp. 65-69; also in 'Boll. Acad. Gioenia, Catania,' Fasc. 89, pp. 15-19.



Nuttall (l. c.) records a personal communication of Stiles, who placed the larvæ of *Musca* with female *Ascaris lumbricoides*, which they devoured together with the eggs contained by the nematodes. The larvæ and adult flies contained the eggs of the *Ascaris*, and as the weather at the time of the experiment was very hot the *Ascaris* eggs developed rapidly and were found in different stages of development in the insect, thus proving, as Nuttall points out, "that the latter may serve as disseminators of the parasite." These experiments of Grassi and Stiles show that flies can act as carriers of the eggs of these parasitic worms, and that man could be infected by the fly depositing its excreta on his food, or being accidentally immersed in food as flies frequently are.

#### VII. THE DISSEMINATION OF PATHOGENIC ORGANISMS BY *MUSCA DOMESTICA* AND ITS NON-BLOOD-SUCKING ALLIES.

Although *M. domestica* is unable to act as a carrier of pathogenic micro-organisms in a manner similar to that of the mosquito, so far as we know at present, nevertheless its habits render it a very potent factor in the dissemination of disease by the mechanical transference of the disease germs. These habits are the constant frequenting and liking for substances used by man for food on the one hand and excremental products, purulent discharges, and moist surfaces on the other. Should these last contain pathogenic bacilli, the proboscis, body, and legs of the fly are so densely setaceous (see fig. 20) that a great opportunity occurs, with a maximum amount of probability, for the transference of the organisms from the infected material to either articles of food or such moist places as the lips, eyes, etc. As I have already pointed out (1907), *M. domestica* is unable to pierce the skin, as certain persons have suggested. The structure of the proboscis will not permit the slightest piercing or pricking action, which fact eliminates such an inoculative method of infection. It is as a mechanical carrier, briefly, that *M.*

*domestica* and such allies as *H. canicularis*, etc., though to a less degree, may be responsible for the spread of infectious disease of a bacillary nature, and an account will now be given of the rôle which this insect plays in the dissemination of certain diseases.<sup>1</sup> Before doing so, however, it should be pointed out that whereas in some of the diseases the epidemiological evidence adduced in support of the transference of disease germs by flies is confirmed bacteriologically, in others only the former evidence exists. Should neither form of evidence be available in support of the idea that *M. domestica* plays a part in the dissemination of the infection of a particular disease, it is essential, nevertheless, that if such a method of transference is possible the potency of this insect should be realised. This potency is governed by such factors as the presence of *M. domestica*; its access to the infected or infective material, this being attractive to the insect either because it is moist or because it will serve as food for itself or its progeny; and a certain power of resistance for a short time against desiccation on the part of the pathogenic organisms, although, as in the case of the typhoid bacillus, the absence of this factor is not fatal to the idea, as it may be overcome by the fact that the fly is able to take on its appendages an amount sufficient to resist desiccation for a short time. The last factor is the presence of suitable culture media, such as certain foods, or moist surfaces as the mouth, eyes, or wounds, for the reception of the organisms which have been carried on the body or appendages of the fly. If these conditions are satisfied the possibility of *M. domestica* or its allies playing a part in the transference of the infection should be carefully considered, and this suggestive evidence will be discussed in certain of the diseases which follow, in addition to the epidemiological and bacteriological evidence.

<sup>1</sup> Though it should be unnecessary, I wish to explain, as I have been occasionally misunderstood by medical men and others, that *M. domestica* is not regarded as being the cause of any disease, but as a carrier of the infection.

### 1. Typhoid Fever.

Of all infectious diseases the conditions in this are most favourable for the transference of infection by *M. domestica*, and it is no doubt on this account that the greatest attention has been paid to the rôle of house-flies in the dissemination of this disease. The chief favourable condition is that the typhoid bacillus occurs in the stools of typhoid and incipient typhoid cases. Human excrement attracts flies not only on account of its moisture but as suitable food for the larvæ. The infected excrement is often accessible to flies, especially in military camps, as will be shown shortly, and the flies also frequent articles of food and not infrequently the moist lips of man. Such are the conditions most suitable for the transference of the bacilli, and it is on account of the frequent coincidence of these conditions that flies can play, and have played, such an important rôle in the dissemination of this disease among communities, in spite of the fact that the typhoid bacillus cannot survive desiccation, which I think is an argument against its being carried by dust.

Epidemiological and other evidence.—There is a very large amount of testimony given as to the rôle played by flies in the spread of enteric in military stations and camps, and especially during the two wars—the Spanish-American and the Boer War. All the conditions most favourable for the dissemination of the bacilli by flies were, and in many military stations are still, present; open latrines or filth-trenches accessible to flies on the one hand and on the other the men's food within a short distance of the latrines. I cannot do better than repeat the evidence in the words of the witnesses and allow it to speak for itself.

Vaughan, a member of the U.S. Army Typhoid Commission of 1898, states:<sup>1</sup>

“My reasons for believing that flies were active in the dissemination of typhoid fever may be stated as follows:

<sup>1</sup> In a paper, “Conclusions Reached after a Study of Typhoid Fever among American Soldiers,” read before the American Medical Association at Atlantic City, N.J., in 1900.

“(a) Flies swarmed over infected faecal matter in the pits and then visited and fed upon the food prepared for the soldiers in the mess-tents. In some instances where lime had recently been sprinkled over the contents of the pits, flies with their feet whitened with lime were seen walking over the food.

“(b) Officers whose mess-tents were protected by screens suffered proportionately less from typhoid fever than did those whose tents were not so protected.

“(c) Typhoid fever gradually disappeared in the fall of 1898 with the approach of cold weather and the consequent disabling of the fly.

“It is possible for the fly to carry the typhoid bacillus in two ways. In the first place faecal matter containing the typhoid germs may adhere to the fly and be mechanically transported. In the second place, it is possible that the typhoid bacillus may be carried in the digestive organs of the fly and may be deposited with its excrement.”

One of his conclusions was that infected water was not an important factor in the dissemination of typhoid in the national encampments of 1898, since only about one fifth of the soldiers in the national encampments during the summer of that year developed typhoid fever, whereas about 80 per cent. of the total deaths were due to this disease. In the latter connection Sternberg (1899) refers to a report of Dr. Reed upon an epidemic in the Cuban War, in which it was stated that the epidemic was clearly not due to water infection but was transferred from the infected stools of the patients to the food by means of flies, the conditions being especially favourable for this means of dissemination. Sternberg, as Surgeon-General of the U.S. Army, issued the following instructions<sup>1</sup>: “Sinks should be dug before a camp is occupied or as soon after as practicable. The surface of the faecal matter should be covered with fresh earth or quicklime or ashes three times a day.” I think that the instructions of that ancient leader of men, Moses, who probably had

<sup>1</sup> ‘Circular No. 1 of the Surgeon-General of the U.S. Army.’ April, 1898.

experienced the effects of flies, were even better than these. He said (Deut., Ch. xxiii, v. 12-13): "Thou shalt have a place also without the camp whither thou shalt go forth abroad; and thou shalt have a paddle [or 'shovel'] among thy weapons; and it shall be, when thou sittest down abroad, thou shalt dig therewith, and shalt turn back and cover that which cometh from thee."

Sternberg is of the opinion that typhoid fever and camp diarrhœa are frequently communicated to soldiers through the agency of flies, "which swarm about fæcal matter and filth of all kinds deposited upon the ground or in shallow pits, and directly convey infectious material attached to their feet or contained in their excreta to the food which is exposed while being prepared in the common kitchen, or while being served in the mess-tent."

Veeder (1898), in referring to the conditions existing in the camps of the Spanish-American war, says that in the latrine trenches he saw "fæcal matter fresh from the bowel and in its most dangerous condition, covered with myriads of flies, and at a short distance there was a tent, equally open to the air, for dining and cooking. To say that the flies were busy travelling back and from between these two places is putting it mildly." Further, he says, "There is no doubt that air and sunlight kill infection, if given time, but their very access gives opportunity for the flies to do serious mischief as conveyers of fresh infection wherever they put their feet. In a very few minutes they may load themselves with the dejections from a typhoid or dysenteric patient, not as yet sick enough to be in hospital or under observation, and carry the poison so taken up into the very midst of the food and water ready for use at the next meal. There is no long and round-about process involved. It is very plain and direct. Yet when the thousands of lives are at stake in this way the danger passes unnoticed, and the consequences are disastrous and seem mysterious until attention is directed to the point; then it becomes simple enough in all conscience."

The Commission which investigated the outbreaks of



enteric fever that occurred in 1898 in the United States during this war came to the conclusion that "flies undoubtedly served as carriers of the infection" under the conditions which have already been described. Many other authorities bear witness to the same facts.

In our own South African war, a year or two later, the same conditions existed, and there was a very heavy loss of life from enteric fever. Writing on the subject, Dunne (1902) says: "The plague of flies which was present during the epidemic of enteric at Bloemfontein in 1900 left a deep impression on my mind, and, as far as I can ascertain from published reports, on all who had experience on that occasion. Nothing was more noticeable than the fall in the admissions from enteric fever coincident with the killing off of the flies on the advent of the cold nights of May and June. In July, when I had occasion to visit Bloemfontein, the hospitals there were half empty, and had practically become convalescent camps." A similar experience is related by Tooth (1901). Referring to the rôle of flies he says: "As may be expected, the conditions in these large camps were particularly favourable to the growth and multiplication of flies, which soon became terrible pests. I was told by a resident in Bloemfontein that these insects were by no means a serious plague in ordinary times, but that they came with the army. It would be more correct to say that the normal number of flies was increased owing to the large quantities of refuse upon which they could feed and multiply. They were all over our food, and the roofs of our tents were at times black with them. It is not unreasonable to look upon flies as a very possible agency in the spreading of the disease, not only abroad but at home. It is a well-known fact that with the first appearance of the frost enteric fever almost rapidly disappears. . . . It seems hardly credible that the almost sudden cessation of an epidemic can be due to the effect of cold upon the enteric bacilli only. But there can be no doubt in the mind of anybody who has been living on the open veldt, as we have for three or four months, that flies are ex-



tremely sensitive to the change of temperature, and that the cold nights kill them off rapidly." In the discussion on this paper Church stated that "many nurses told me that if one went into a tent or ward in which the patients were suffering from a variety of diseases, one could tell at once which were the typhoid patients by the way in which the flies clustered about their mouths and eyes while in bed." It was further stated in the discussion that where the Americans used quicklime in their latrines the cooks in the neighbouring kitchens found that the food became covered with quicklime from the flies which came from the latrines to the kitchens.

Dr. Tooth, in a letter to me, says: "I am afraid my written remarks hardly express strongly enough the importance that I attach to flies as a medium of spreading infection. Of course I do not wish to under-rate the water side of the question, but once get, by that means, enteric into a camp the flies, in my opinion, are quite capable of converting a sporadic incidence into an epidemic. A pure water supply is an obvious necessity, but the prompt destruction of refuse of every description is every bit as important."

Smith (1903), in speaking of his experiences in South Africa, says that: "On visiting a deserted camp during the recent campaign it was common to find half a dozen or so open latrines containing a foetid mass of excreta and maggots." Similar observations were made by Austen (1904), who, describing a latrine that had been left a short time undisturbed, says: "A buzzing swarm of flies would suddenly arise from it with a noise faintly suggestive of the bursting of a percussion shrapnel shell. The latrine was certainly not more than one hundred yards from the nearest tents, if so much, and at meal-times men's mess-tins, etc., were always invaded by flies. A tin of jam incautiously left open for a few minutes became a seething mass of flies (chiefly *Pycnosoma chloropyga* Wied), completely covering the contents."

Howard (1900) referring to an American camp, where no effort was made to cover the faeces in the latrines, says: "The camp contained about 1200 men, and flies were extremely

numerous in and around the sinks. Eggs of *Musca domestica* were seen in large clusters on the faeces, and in some instances the patches were two inches wide and half an inch in depth, resembling little patches of lime. Some of the sinks were in a very dirty condition and had a very disagreeable odour."

A few examples of the prevalence of conditions favouring the dissemination of enteric by flies in permanent camps may be noted. Cockerill (1905), in describing camp conditions in Bermuda, mentions kitchens within one hundred yards of the latrines; the shallow privy, seldom or never cleaned out, and middens are found which contain masses of filth swarming with flies. He states that in more recent years the period of greatest incidence is in the summer, being chiefly due to flies and contaminated dust. Quill (1900), reporting on an outbreak of enteric in the Boer camp in Ceylon, states: "During the whole period that enteric fever was rife in the Boer camp flies in that camp amounted to almost a plague, the military camp being similarly infested, though to a less extent. The outbreak in the Boer camp preceded that among the troops; the two camps were adjacent, and the migration of the flies from the one to the other easy." Weir, reporting on an outbreak of enteric fever in the barracks at Umbala, India,<sup>1</sup> says that most of the pans in the latrines were half or quite full, and flies were very numerous in them and on the seats, which latter were soiled by the excreta conveyed by the flies' legs. The men stated that the plague of flies was so great that in the morning they could hardly go to the latrines. He found that the flies were carried from the latrines to the barrack-rooms on the clothes of the men. This state of affairs suggests another mode of infection, namely, per rectum. As Smith has pointed out (l.c.) it is not improbable that flies under these conditions may be inoculators of dysentery.

Aldridge (1907) gives some interesting statistics showing the influence of the presence of breeding-places of flies. Flies are found in greater numbers in mounted regiments than in

<sup>1</sup> 'Army Medical Department Report,' 1902, p. 207.

infantry, and he shows how this affects the incidence of enteric fever. In the British Army in India, 1902-05, the ratios per 1000 per annum of cases admitted were: cavalry 41.1, and infantry 15.5; and in the U.S. Army were: cavalry 5.74, and infantry 4.75. He states that: "A study of the incidence of enteric fever shows that stations where there are no filth trenches, or where they are a considerable distance from the barracks, all have an admission-rate below the average, and all but one less than half the average."

All these facts are equally applicable to the conditions in our own towns and cities. Where the old conservancy methods are used, such as pails and privy middens, the incidence of typhoid fever is greater than in those places where the system of water disposal has been adopted. I have examined the annual reports of the medical officers of health of several large towns where such conversions are being made, and they show a falling-off of the typhoid fever-rate coincident with this change. In Nottingham, for example,<sup>1</sup> in the ten years 1887-1896, there was one case of typhoid fever for every 120 houses that had pail-closets, one case for every 37 houses with privy middens, and one case for every 558 houses with water-closets. The last were scattered, and not confined to the prosperous districts of the town.

One of the most important investigations on the relation of flies to intestinal disease was that of Jackson (1907). He investigated the sanitary condition of New York harbour and found that in many places sewer outfalls had not been carried below low-water mark, consequently solid matter from the sewers was exposed on the shores, and that during the summer months on and near the majority of the docks in the city a large amount of human excreta was deposited. This was found to be covered with flies. The report, considered as a mere catalogue, is a most severe indictment against the insanitary condition of this great water front. By means of spot-maps he shows that the cases of typhoid are thickest

<sup>1</sup> "Typhoid Fever and the Pail System at Nottingham," 'Lancet,' November 29th, 1902, p. 1489.

near the points found to be most insanitary. He shows, as English investigators have also shown, how the curves of fatal cases correspond with the temperature curves and with the curves of the activity and prevalence of flies which were obtained by actual counts. He also adduced bacteriological evidence, and it is stated that one fly was found to be carrying over one hundred thousand faecal bacteria.

Bacteriological evidence.—In addition to the evidence of Jackson, to which reference has been made, further proof that flies are able to carry the typhoid bacillus has been available for some years. Celli (1888) recovered the *Bacillus typhi abdominalis* from the dejections of flies which had been fed on cultures of the same, and he was able to prove that they passed through the alimentary tract in a virulent state by subsequent inoculation experiments. Ficker (1903) found that when flies were fed upon typhoid cultures they could contaminate objects upon which they rested. The typhoid bacilli were present in the head and on the wings and legs of the fly five days after feeding, and in the alimentary tract nine days after. Firth and Horrocks (1902), in their experiments, took a small dish containing a rich emulsion in sugar made from a twenty-four-hour agar slope of *Bacillus typhosus* recently obtained from an enteric stool and rubbed up with fine soil. This was introduced with some infected honey into a cage of flies together with sterile litmus agar plates and dishes containing sterile broth, which were placed at a short distance from the infected soil and honey. Flies were seen to settle on the infected matter and on the agar and broth. The agar plates and broth were removed after a few days, and after incubation at 37° C. for twenty-four hours colonies of *Bacillus typhosus* were found on the agar plates and the bacillus was recovered from the broth. In a further experiment the infected material was dusted over with fine earth to represent superficially buried dejecta, and the bacillus was isolated from agar plates upon which the flies had subsequently walked, as in the former experiment. They also found the bacillus on the heads, wings,

legs and bodies of flies which had been allowed to have access to infected material. Hamilton (1903) recovered *Bacillus typhosus* five times in eighteen experiments from flies caught in two undrained privies, on the fences of two yards, on the walls of two houses and in the room of an enteric fever patient. A series of careful experiments were made by Sellars<sup>1</sup> in connection with Niven's investigations on the relation of flies to infantile diarrhœa. Out of thirty-one batches of house-flies carefully collected in sterilised traps in several thickly populated districts in Manchester he found, as a result of cultural and inoculatory experiments, that bacteria having microscopical and cultural characters resembling those of the *Bacillus coli* group were present in four instances, but they did not belong to the same kind or variety. Buchanan (1907) was unable to recover the bacilli from flies taken from the enteric ward of the Glasgow Fever Hospital. Flies were allowed to walk over a film of typhoid stool and then transferred to the medium (Grünbaum and Hume's modification of MacConkey's medium), and subsequently allowed to walk over a second and a third film of medium. Few typhoid bacilli were recovered and none from the second and third films. Sangree (1899) performed somewhat similar experiments to those of Buchanan and recovered various bacilli in the tracks of the flies. This method of transferring the flies immediately from the infected material to the culture plate is not very satisfactory, as I have already pointed out (1908), as it would be necessary for the flies to be very peculiarly constructed not to carry the bacilli. The fly should be allowed some freedom before it has access to the medium to simulate natural conditions. Experiments of this kind were carried out in the summer of 1907 by Dr. M. B. Arnold (superintendent of the Manchester Fever Hospital) and myself. Flies were allowed to walk over a film of typhoid stool and then were transferred to a wire cage, where they remained for twenty-four hours with the opportunity

<sup>1</sup> Recorded in the 'Report on the Health of the City of Manchester, 1906,' by James Niven, pp. 86-96.



of cleaning themselves, after which they were allowed to walk over the films of media. Although we were unable to recover *B. typhosus* the presence of *B. coli* was demonstrated. *B. coli* was also obtained from flies obtained on a public tip upon which the contents of pail-closets had been emptied; the presence of *B. coli*, however, may not necessarily indicate recent contamination with human excrement. Aldridge (l.c.) isolated a bacillus apparently belonging to the paratyphoid group from flies caught in a barrack latrine in India during an outbreak of enteric fever. In appearance and behaviour to tests it was very similar to *B. typhosus*.

Although we are not certain yet as to the specific organism or organisms which cause the intestinal disease known as infantile or summer diarrhoea, which is so prevalent during the summer months and is responsible for so great a mortality among young children, I think we must consider the relationship of *M. domestica* and its ally *Homalomyia canicularis* to this disease epidemiologically similar to typhoid fever.

## 2. Anthrax.

In considering the relation of flies to anthrax several facts should be borne in mind. As early as the eighteenth century it was believed that anthrax might result from the bite of a fly, and the idea has been used by Murger in his romance 'Le Sabot Rouge.' A very complete historical account of this is given by Nuttall (1899). Most of the instances in support of this belief, however, that flies may carry the infection of anthrax, refer to biting flies. As I have already pointed out, *M. domestica* and such of its allies as *H. canicularis*, *C. erythrocephala*, *C. vomitoria*, and *Lucilia cæsar* are not biting or blood-sucking flies. The nearest allies of *M. domestica* which suck blood in England are *S. calcitrans*, *Hæmatobia stimulans* Meigen, and *Lyperosia irritans* L.; the rest of the blood-sucking flies which may be considered in this connection belong to the family Tabanidæ, including the common genera *Hæma-*



lopota, *Tabanus*, and *Chrysops*. These biting and blood-sucking flies live upon the blood of living rather than dead animals. But it is from the carcasses and skins of animals which have died of anthrax that infection is more likely to be obtained, and I believe that such flies as the blow-flies (*Calliphora* spp.), and sometimes *M. domestica* and *Lucilia cæsar*, which frequent flesh and the bodies of dead animals for the purpose of depositing their eggs and for the sake of the juices, are more likely to be concerned in the carriage of the anthrax bacillus and the causation of malignant pustule than are the blood-sucking flies. Consequently, as *M. domestica* and its allies only are under consideration, and for the sake of brevity, the relation to anthrax of the non-biting flies only will be considered here.

The earliest bacteriological evidence in support of this belief was published by Raimbert (1869). He experimentally proved that the house-fly and the meat-fly were able to carry the anthrax bacillus, which he found on their probosces and legs. In one experiment two meat-flies were placed from twelve to twenty-four hours in a bell-jar with a dish of dried anthrax blood. One guinea-pig was inoculated with a proboscis, two wings and four legs of a fly, and another with a wing and two legs. Both were dead at the end of sixty hours, anthrax bacilli being found in their blood, spleen, and heart. He concludes: "Les mouches qui se posent sur les cadavres des animaux morts du Charbon sur les dépouilles, et s'en nourrissent, ont la faculté de transporter les virus charbonneux déposé sur la peau peut en traverser les différentes couches." Davaine (1870) also carried out similar experiments with *C. vomitoria*, which was able to carry the anthrax bacillus. Bollinger (1874) found the bacilli in the alimentary tract of flies that he had caught on the carcase of a cow dead of anthrax. Buchanan (l. c.) placed *C. vomitoria* under a bell-jar with the carcase of a guinea-pig (deprived of skin and viscera) which had died of anthrax. He then transferred them to agar medium and a second agar capsule, both of which subsequently showed a profuse growth

of *B. anthracis* as one might expect. Specimens of *M. domestica* were also given access to the carcase of an ox which had died of anthrax; they all subsequently caused growths of the anthrax bacillus on agar. I entirely agree with Nuttall, who says: "It does seem high time, though, after nearly a century and a half of discussion, to see what would be the result of properly carried out experiments. That ordinary flies (*M. domestica* and the like) may carry about and deposit the bacillus of anthrax in their excrements, or cause infection through their soiled exterior coming in contact with wounded surfaces or food, may be accepted as proven in view of the experimental evidence already presented."

### 3. Cholera.

One of the first to suggest that flies may disseminate the cholera spirillum was Nicholas (1873), who, in an interesting and prophetic letter, said: "In 1849, on an occasion of going through the wards of the Malta Hospital, where a large amount of Asiatic cholera was under treatment, my first impression of the possibility of the transfer of the disease by flies was derived from the observation of the manner in which these voracious creatures, present in great numbers, and having equal access to the dejections and food of the patients, gorged themselves indiscriminately, and then disgorged themselves on the food and drinking utensils. In 1850 the 'Superb,' in common with the rest of the Mediterranean squadron, was at sea for nearly six months; during the greater part of the time she had cholera on board. On putting to sea the flies were in great force, but after a time the flies gradually disappeared and the epidemic slowly subsided. On going into Malta Harbour, but without communicating with the shore, the flies returned in greater force, and the cholera also with increased violence. After more cruising at sea the flies disappeared gradually, with the subsidence of the disease. In the cholera years of 1854 and 1866 in this country the periods of occurrence and disappear-

ance of the epidemics were coincident with the fly-season." Buchanan (1897), in a description of a gaol epidemic of cholera which occurred at Burdwan in June, 1896, states that swarms of flies occurred about the prison, outside which there were a number of huts containing cholera cases. Numbers of flies were blown from the sides where the huts lay into the prison enclosure, where they settled on the food of the prisoners. Only those prisoners who were fed in the gaol enclosure nearest the huts acquired cholera, the others remaining healthy.

Bacteriological evidence.—Maddox (1885) appears to have been the first to conduct experiments with a view to demonstrating the ability of flies to carry the cholera spirillum, or, as it was then called, the "comma-bacillus." He fed the flies *C. vomitoria* and *Eristalistenax* (the "drone-fly") on pure and impure cultures of the spirillum, and appears to have found the motile spirillum in the fæces of the flies. He concludes that these insects may act as disseminators of cholera. During a cholera epidemic Tizzoni and Cattani (1886) showed experimentally that flies were able to carry the "comma-bacillus" on their feet. They also obtained, in two out of three experiments, the spirillum from cultures made with flies from one of the cholera wards. Sawtchenko (1892) made a number of careful experiments. Flies were fed on bouillon culture of the cholera spirillum, and to be certain that the subsequent results should not be vitiated by the presence of the spirillum on the exterior of the flies, he disinfected them externally and then dissected out the alimentary canal, with which he made cultures. In the case of flies which had lived for forty-eight hours after feeding, the second and third cultures represented pure cultures of the cholera spirillum. Simmonds (1892) placed flies on a fresh cholera intestine, and afterwards confined them from five to forty-five minutes to a vessel in which they could fly about. Roll cultures were then made, and colonies of the cholera spirillum were obtained after forty-eight hours. Colonies were also obtained from a fly one and a half hours after having

access to a cholera intestine, and also from flies caught in a cholera post-mortem room. Uffelmann (1892) fed two flies on liquefied cultures of the cholera spirillum, and after keeping one of them for an hour in a glass he obtained 10,500 colonies from it by means of a roll culture; from the other, which was kept two hours under the glass, he obtained twenty-five colonies. In a further experiment he placed one of the two flies similarly infected with the spirillum in a glass of sterilised milk, which it was allowed to drink. The milk was then kept for sixteen hours at a temperature of 20-21° C., after which it was shaken, and cultures were made from it; one drop of milk yielded over one hundred colonies of the spirillum. The other fly was allowed to touch with its proboscis and feed upon a piece of juicy meat that was subsequently scraped. From one half of the surface twenty colonies, and from the other half one hundred colonies, of the spirillum were obtained. These experiments show the danger which may result if flies having access to a cholera patient, and bearing the spirillum, have access also to the food. Macrae (1894) records experiments in which boiled milk was exposed in different parts of the gaol at Gaya in India, where cholera and flies were prevalent. Not only did this milk become infected, but the milk placed in the cowsheds also became infected. The flies had access both to the cholera stools and to such food as rice and milk.

These foregoing experiments prove beyond doubt the ability of flies to carry the cholera spirillum, both internally and externally, in a virulent condition, and to infect food.

#### 4. Tuberculosis.

Although it may be considered to be hardly necessary to introduce flies as a means of disseminating the tubercle bacillus, it has, nevertheless, been proved experimentally that they are able to carry the bacillus in a virulent condition. As early as 1887 Spillman and Hanshalter carried on experiments in which they found the tubercle bacillus in large

numbers in the intestines of flies from a hospital ward, and also in the dejections which occurred on the windows and walls of the ward. Hoffmann (1886) also found tubercle bacilli in the excreta of flies in the room where a patient had died of tuberculosis, and he also found the bacilli in the intestinal contents. One out of three guinea-pigs which were inoculated with the intestines died; two inoculations with the excreta had no effect, which led him to believe that the bacilli became less virulent in passing through the alimentary tract. But Celli (l. c.) records experiments in which two rabbits inoculated with the excreta of flies fed with tubercular sputum developed the disease. Hayward (1904) obtained tubercle bacilli in ten out of sixteen cultures made from flies which had been caught feeding on bottles containing tuberculous sputum. Tubercle bacilli were also recovered from cultures made from the fæces of flies which had fed in the same manner, which apparently caused a kind of diarrhœa in the flies, and they died from two to three days afterwards. Fæces of flies fed on tubercular sputum were rubbed up in sterile water and injected into the peritoneal cavity of guinea-pigs, which developed tuberculosis. Buchanan (l. c.) allowed flies to walk over a film of tubercular sputum and then over agar; a guinea-pig died of tuberculosis in thirty-six days by inoculating it with the resulting culture.

### 5. Ophthalmia.

Flies have been suggested as playing an important part in the spread of conjunctivitis, especially Egyptian ophthalmia, and although, so far as I have been able to discover, we have no bacteriological evidence in favour of the belief, the circumstantial evidence is sufficiently strong to warrant it.

In speaking of its occurrence at Biskra, Laveran (1880) says that in the hot season the eyelids of the indigenous children are covered with flies, to the attentions of which they submit; in this way the infectious discharge is carried on the legs and probosces of flies to the healthy children.



Dr. Andrew Balfour, of the Gordon College, Khartoum, in a letter to me, says that the Koch-Weeks bacillus is generally recognised as being the exciting cause of Egyptian ophthalmia. He says, "Ophthalmia is not nearly so common in the Sudan as in Egypt, nor are flies so numerous; doubtless the two facts are associated." Dr. MacCallan, of the Egyptian Department of Public Health, in answer to my inquiries, says that acute ophthalmias are more liable to transmission by flies than is trachoma. In his opinion the spread of the latter is, to a comparatively small extent, through the agency of flies, but it is mainly effected by direct contact of the fingers, clothes, etc.

The Koch-Weeks bacillus was first seen by Koch (1883) in Egypt in cases of acute catarrhal ophthalmia. He found that two distinct diseases were referred to under the name; in the severe purulent form he found diplococci, which he identified as very probably *Gonococci*; in the more catarrhal form he found small bacilli in the pus-corpuscles. He ascribed the propagation of the disease to flies, which were often seen covering the faces of children. Axenfeld (1908) states that "almost the only organisms occurring in acute epidemics of catarrhal conjunctivitis are the Koch-Weeks bacillus (perhaps also influenza bacillus), and the pneumococcus (in Egypt the gonococcus also, rarely *subtilis*). Other pathogenic conjunctival organisms<sup>1</sup> only exceptionally occur." And, further, "*Gonococci* and Koch-Weeks bacilli evidently lose their power of causing a conjunctivitis very slowly indeed, and are very independent of any disposition." His statement that, "on account of their great virulence and the marked susceptibility to them, a very small number suffices," is important in considering the relation of flies to the spread of the disease, although, as he remarks, every infection does not produce the disease. The fact that the Koch-Weeks bacillus cannot resist dryness cannot be urged as an argument

<sup>1</sup> In this connection he states (p. 236): "We can make the general statement that the staphylococcus in the conjunctiva is not contagious."



against the spread of the infection by flies, or the same would apply to the typhoid bacillus, whose carriage by flies is proven. Axenfeld mentions L. Müller and Lakah and Khouri as advocating the view that flies may spread the infection more readily. In view of the fact that, as the same author states, "Koch-Weeks conjunctivitis is to be classed with the most contagious infectious disease which we know of," it is important that the rôle of flies should be fully recognised. Notwithstanding the occurrence in this country of flies in less numbers than in such countries as Egypt, it would be well to bear in mind the probable influence of flies in cases of acute conjunctivitis, such as those described by Stephenson (1897) in our own country. The sole difference between the disease in Egypt and here is, as Dr. Bishop Harman points out to me in a letter, that "the symptoms produced (in Egypt) are, from climate and dirtiness of the subjects, more severe, and that there is found a greater number of cases of gonorrhœal disease than in England"; and, I would add, a far greater number of flies. This disease is eminently suited for dissemination by flies, both on account of the accessibility of the infectious matter in the form of a purulent discharge from the eyes and on account of the flies' habit of frequenting the eyes.

## 6. Plague.

Although fleas are considered to be the chief agents in the dissemination of the plague bacillus in spite of the fact that the proof is not absolutely convincing, it is nevertheless interesting, and certainly not unimportant, to refer to the series of experiments of Nuttall (1897) on *M. domestica*. In these experiments he conclusively proved that flies were able to carry the plague bacillus, and that they subsequently died of the disease. Flies were fed upon the crushed organs of animals which had died of plague. Control flies were fed in a similar manner on the organs of uninfected animals, and the control experiments were kept under the same conditions.

In two of the experiments the flies were all dead on the seventh and eighth days respectively, at a temperature of  $14^{\circ}$  C. At higher temperatures he found that flies died more rapidly. He was able to show that the flies contained the bacilli in a virulent condition for about two days after they had fed on infected organs; this, and the fact that the infected flies can live for several days, are extremely important from the practical standpoint, as indicating that flies should neither be allowed to have access to the bodies or excreta of cases of plague, nor to the food.

## 7. Miscellaneous.

There are on record a number of suggestions that flies may be responsible for the dissemination of other diseases caused by bacteria and other micro-organisms, and some account will now be given of these and the experiments in support of such beliefs.

If flies have access to wounds of an inflammatory and suppurative nature they are liable to transport the *Staphylococci* to other spots. Buchanan (1907) allowed *M. domestica* to walk over a film of *Staphylococcus pyogenes aureus* from an abscess, and afterwards over agar; a mixed growth resulted, in which *S. pyogenes aureus* predominated. Celli (l.c.) records experiments which proved that *S. pyogenes aureus* retains its virulence after passing through the intestine of the fly.

In the experiments carried out in 1907 by my friend Dr. M. B. Arnold and myself, he chose *B. prodigiosus* for the purposes of the experiment, as it is easily recognisable and not likely to be accidentally introduced. Flies which had just emerged from the pupæ, and therefore not already contaminated with an extensive bacterial flora, were allowed to walk over a film of the bacillus, after which they were confined to sterile glass tubes. At varying periods they were taken out and allowed to walk over the culture plates. Those confined for over twelve hours retained the bacilli on their

TABLE SHOWING SOURCES OF BACTERIA FROM FLIES.

Date.	Source.	Total number of bacteria.	Total acid bacteria.	Rapid liquefying bacteria.	Slow liquefying bacteria.	<i>Bacterium lactis acid.</i> Group A, Class 1.	<i>Coli aerogenes.</i> Group A, Class 2.
1907							
July 27	(a) 1 fly, bacteriological laboratory	3,150	250	600	100	—	—
" 27	(b) 1 fly, bacteriological laboratory	550	100	—	—	—	—
Aug. 6	(c) 19 cow-stable flies	7,980,000	220,000	—	20,000	—	—
" 14	Average per fly	420,000	11,600	—	1,000	—	—
" 14	(d) 94 swill-barrel flies	155,000,000	8,950,000	—	—	4,320,000	4,630,000
" 14	Average per fly	1,660,000	95,300	—	—	46,000	49,300
" 14	(e) 144 pig-pen flies	133,000,000	2,110,000	100,000	266,000	933,000	1,176,000
" 14	Average per fly	923,000	18,700	700	1,150	6,500	12,000
Sept. 4	(f) 18 swill-barrel flies	118,800,000	40,480,000	—	14,500,000	10,480,000	30,000,000
" 21	Average per fly	6,600,000	2,182,000	—	804,000	582,000	1,600,000
" 21	(g) 30 dwelling-house flies	1,425,000	125,000	—	12,500	—	—
" 21	Average per fly	47,580	4,167	—	417	—	—
" 27	(h) 26 dwelling-house flies	22,880,000	22,596,000	120,000	34,000	—	—
" 27	Average per fly	880,000	869,000	4,600	1,300	—	—
" 27	(i) 110 dwelling-house flies	35,500,000	13,670,000	8,840,000	125,000	—	—
" 27	Average per fly	322,000	124,200	80,300	1,100	—	—
Aug. 20	(j) 1 large blue-bottle blowfly	308,700	(a)	—	—	—	—
	Total average of 414 flies	1,222,570	367,300	7,830	73,500	—	—
	Average per cent. of 414 flies	—	30	6	6	—	—
	Average per fly of 256 flies, experiments (d), (e), and (f)	3,061,000	765,000	230	268,700	211,500	553,800
	Average per cent. of 256 flies, experiments (d), (e), and (f).	—	25	—	8	7	18

(a) 2200 mould spores.

appendages and transferred them subsequently to the culture media, but they were not recovered from those flies which were kept in confinement for twenty-four hours; a large number of flies, however, were not used.

Dr. Kerr, of Morocco, in a paper on "Some Prevalent Diseases in Morocco," read before the Glasgow Medico-Chirurgical Society (December 7th, 1906), described epidemics of Syphilis where, according to the author, the disease was spread by flies which had been feeding upon the open sores of a syphilitic patient.

Howard (1909) calls attention to an important investigation carried on by Esten and Mason (1908) on the rôle which flies play in the carriage of bacteria to milk. The flies were caught by means of a sterile net; they were then introduced into a sterile bottle and shaken up in a known quantity of sterilised water to wash the bacteria from their bodies and to simulate the number of organisms that would come from a fly falling into a quantity of milk. They summarised their results in the table given on p. 403.

From that table it will be seen that the numbers of bacteria carried by a single fly may range from 550 to 6,600,000, while the average number was about 1,222,000. Commenting on these results, the authors state that "early in the fly-season the numbers of bacteria on flies are comparatively large. The place where flies live also determines largely the numbers that they carry." From these results the importance of keeping flies away from milk and other food will readily be seen.

### VIII. FLIES AND INTESTINAL MYIASIS.

The larvæ of *M. domestica* and its allies are frequently the cause of intestinal myiasis and diarrhœa in children. The occurrence of the larvæ in the human alimentary tract may be accounted for in several ways. The flies may have deposited the eggs on the lips or in the nostrils of the patient, or the eggs may have been deposited on the food, subsequently

passing uninjured either as eggs or as young larvæ into the alimentary tract owing to insufficient mastication. Or the larvæ may have entered per rectum, the eggs having been deposited when the patient was visiting one of the old-style privies where these flies, especially *H. canicularis* and *H. scalaris*, frequently abound. These last two species are frequently the cause of this intestinal trouble, and it is most probable that the larvæ enter per rectum.

Owing to the inability on the part of the observers to distinguish the different species of dipterous larvæ we have little information as to their occurrence in these cases. Stephens (1905) records two cases. Two larvæ were procured which were stated to have been passed per rectum; one was *H. canicularis* and the other is described as *M. corvina*. The latter larva was stated to possess eight lobes on the anterior spiracular processes which "distinguishes these larvæ from *M. domestica*, which has seven only." I suspect this larva was *M. domestica*, which has six to eight lobes on the anterior spiracular processes. Some years ago a number of larvæ which had been passed by a child were sent to this laboratory, and I found that they were *M. domestica*. In 1905 some eggs taken from the stool of a patient suffering from diarrhœa were sent to me and on examination they proved to be the eggs of *C. erythrocephala*. The larvæ of the small house-fly, *H. canicularis*, as I have already mentioned, have occasionally been found in the stools of patients.

In certain cases the larvæ may wander from the mouth or alimentary tract and get into the nasal passages or other ducts, in which cases complications may ensue and result in the death of the patient.

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## X. APPENDIX.

### On the Breeding of *M. domestica* during the Winter Months.

In the account that I gave of the breeding habits of *M. domestica* in the second part of this monograph, it was stated (p. 503) that the experiments and observations pointed to the fact that, in the presence of suitable larval food, such as excremental matter or decaying and fermenting food materials in a moist and warm condition, the female flies would lay their eggs and the larvæ would develop if the temperature of the air was sufficiently high for the prolonged activity of the flies. Flies are sometimes found under these conditions in warm restaurants and kitchens, stables, and cowsheds, and under these conditions are able to breed during the winter months. I am pleased to find that my own observations and those of Griffith (there referred to) as to the ability of *M. domestica* to breed during the winter months has been confirmed by Jepson<sup>1</sup> during the past winter.

Flies were caught in February (1909) in the bakehouse of

<sup>1</sup> In "Reports to the Local Government Board on Public Health and Medical Subjects (New Series, No. 5). Preliminary Reports on Flies as Carriers of Infection. No. 3. Mr. Jepson's Report on the Breeding of the Common House-Fly during the Winter Months," pp. 5-8, 1909.



one of the colleges (Cambridge), and were transferred to a small experimental greenhouse in the laboratory where the temperature was from 65° F. in the morning to 75° F. in the evening. The flies were allowed to oviposit in moist bread in which the process of fermentation had begun. He found that the times for the developmental stages approximately agreed with those obtained by me at about the same temperature, and that the whole development was completed in about three weeks. At an average temperature of 70° F. the eggs were all hatched in twenty-four hours. The first larval stage lasted thirty-six hours, the second larval stage four days, and the third stage was complete in five and a half days; the whole larval period, therefore, occupied eleven days. The average period occupied in the pupal stage was ten days; some pupæ incubated at a temperature of 77° F. hatched in three days.

It may be stated now, therefore, without fear of contradiction, that flies are able to breed during the winter months, if the necessary conditions of food, temperature, and moisture are present. It is probably from these winter flies that the early summer flies are produced, as I have previously suggested.

#### CORRIGENDUM.

My attention has been very kindly called by Prof. W. A. Riley to a slight mistake that I have made in my account of the venation of the wing (Part I, p. 412). By an oversight I have termed transverse nervures the two small veins *m.cu.* (medio-cubital) and *cu.a.* (cubito-anal). These are really parts of the original longitudinal veins *M. 3* and *Cu. 2*. A study of such a series of dipterous wings as those figured by Comstock in the papers there quoted (Comstock and Needham, 1898), or in his 'Manual for the Study of Entomology,' will show that these apparent transverse or cross-veins are morphologically equivalent to branches of the primary veins.

THE UNIVERSITY;  
MANCHESTER.

EXPLANATION OF PLATE 22,

Illustrating Dr. C. Gordon Hewitt's paper on "The Structure, Development, and Bionomics of the House-fly, *Musca domestica*, Linn. Part III. The Bionomics, Allies, Parasites, and the Relations of *M. domestica* to Human Disease."

Fig. 1.—Mature larva of *Homalomyia canicularis*, L.  $\times 17$ . *a.sp.* Anterior spiracular processes. *p.sp.* Posterior spiracular apertures.

Fig. 2.—Posterior end of mature larva of *Anthomyia radicum* Mg. *an.* Anus.

Fig. 3.—Anterior spiracular process of mature larva of *A. radicum*.

Fig. 4.—Head of *Stomoxys calcitrans*, L.: left lateral aspect.

Fig. 5.—Posterior end of mature larva of *S. calcitrans*.

Fig. 6.—Posterior spiracle of the same, enlarged.

Fig. 7.—Posterior spiracle of mature larva of *Musca domestica*.

Fig. 8.—Posterior spiracles of first larval stage of *Calliphora erythrocephala*, Mg.

Fig. 9.—Posterior spiracles of second larval stage of *C. erythrocephala*.

Fig. 10.—Posterior spiracle of mature larva of *C. erythrocephala*.

Fig. 11.—Anterior spiracular process of mature larva of *C. erythrocephala*.

Fig. 12.—Posterior end of mature larva of *C. erythrocephala*.

Fig. 13.—*Chernes nodosus*, Schr.  $\times 30$ .

Fig. 14.—Thoraco-abdominal region of *Homalomyia canicularis*, ♀, showing Gamasids attached to the ventral side of the abdomen.

Fig. 15.—Longitudinal (sagittal) section of abdomen of *M. domestica*, which has been killed by *Empusa muscæ*, showing the feltwork of fungal hyphæ filling the inside of the abdominal cavity and the production of conidia in the intersegmental regions.  $\times 12$ . *c.* Conidiophores producing conidia. *f.* Fungal hyphæ.

Fig. 16.—Four conidiophores showing the formation of conidia (*c.*)  $\times 100$  (approx.).

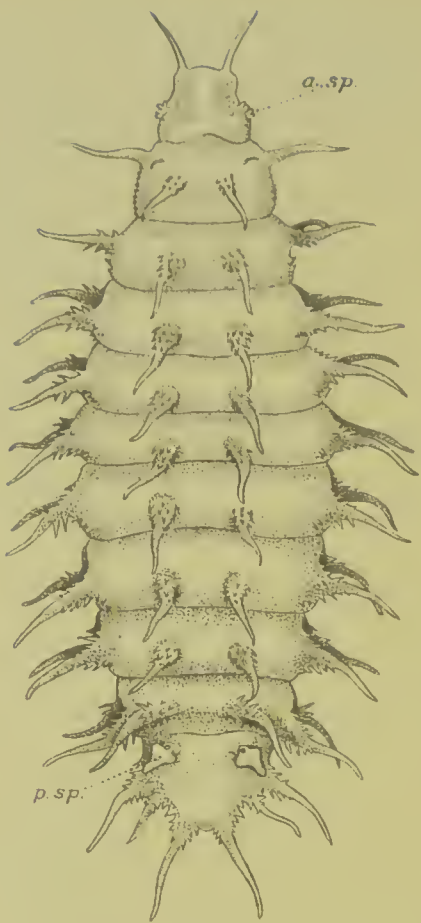
Fig. 17.—Conidium of *Empusa muscæ*.  $\times 400$ . *o.g.* Oil globule.

Fig. 18.—*Habronema muscæ* (Carter). Adult but immature specimen.  $\times 85$ . *g.a.* Genito-anal aperture.

Fig. 19.—Caudal end of *Habronema muscæ*.  $\times 360$ .

Fig. 20.—Tarsal joints of one of posterior pair of legs of *Musca domestica*. Lateral aspect, to show densely setaceous character.





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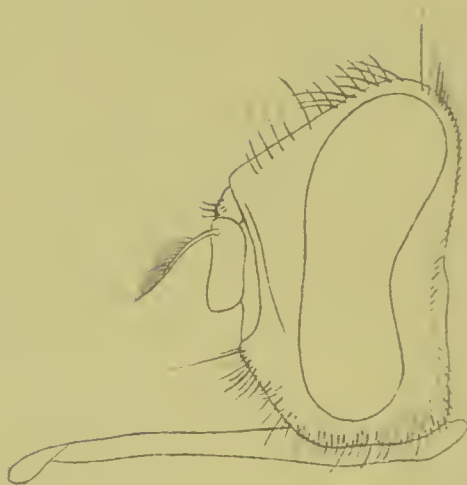
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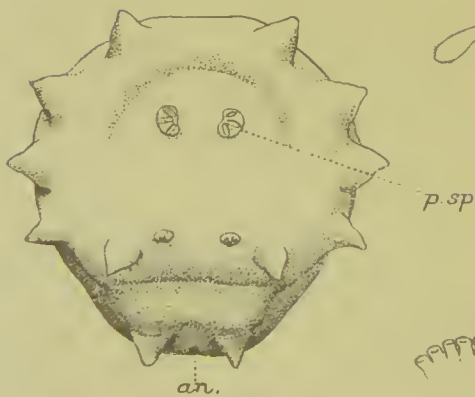


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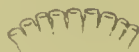
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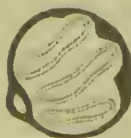
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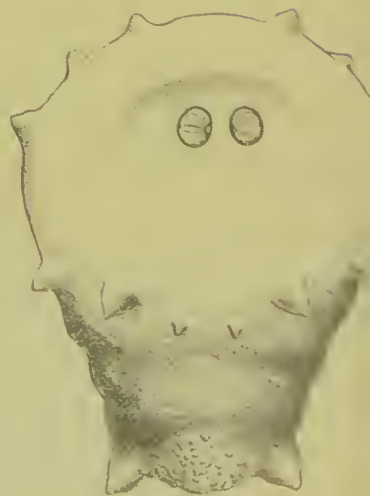
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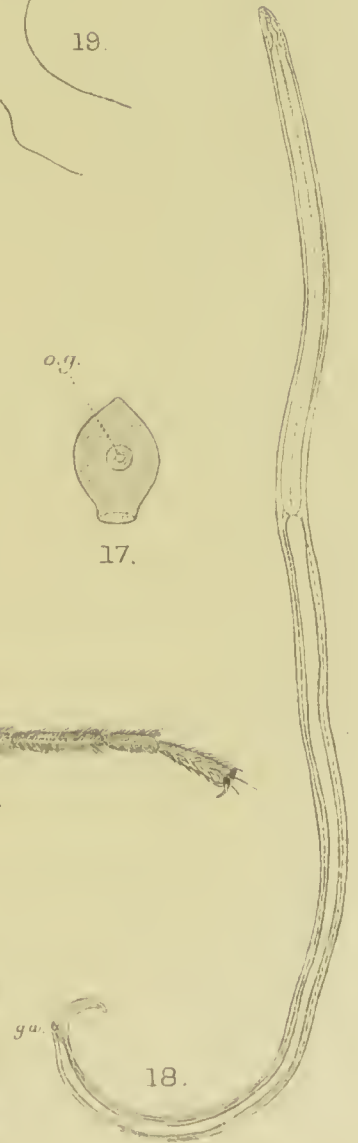
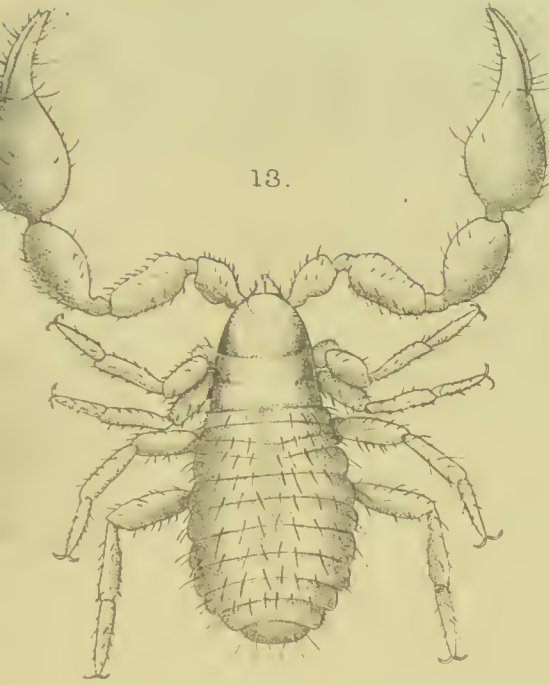
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## XIII. APPENDIX A.

FURTHER OBSERVATIONS ON THE DISSEMINATION OF BACTERIAL AND OTHER ORGANISMS BY *MUSCA DOMESTICA*.

## I. THE RELATION OF FLIES TO SUMMER DIARRHŒA OF INFANTS.

Nash was one of the first medical observers to call attention (in 1902) to the remarkable coincidence between the abundance of flies and the prevalence of this serious infantile disease. In the years 1902 and 1903 the summers were wet and therefore unfavourable to the breeding and activity of *M. domestica*, and in these years the diarrhœal diseases were less prevalent and the infantile mortality rate was considerably below the average. He suggested (1903), in a paper read before the Epidemiological Society of London in January, 1903, that flies carried the infective material from all kinds of filth to the food supplies and were responsible for the spread of this disease and supported his contention with a further instance, namely, that "in the early part of September, 1902, flies became prevalent, and co-incidentally diarrhœa, which had hitherto been conspicuous by its absence, caused thirteen deaths in Southend. Then came a spell of cold weather; the flies rapidly diminished in number, and no further deaths from diarrhœa were recorded" (1905). In 1904, by means of a "spot map," he found that the great majority of deaths from diarrhœa occurred in the proximity of brick fields in which were daily deposited some thirty tons of house refuse, an admirable breeding place for this insect. He has shown the actual

danger which exists in flies carrying bacterial organisms to milk as many other investigators have shown, and the danger resulting from the coincident occurrence of uncovered milk and infected flies is too obvious to need emphasis.

While one regrets that he should feel almost lost, as he states, in the crowd which proclaims far and wide the relation between summer diarrhœa and flies when he had previously felt like one crying in the wilderness (1909, p. 154), it must be acknowledged that Nash did great service in making this fact more widely known when there was so little inclination on the part of medical men to believe it.

The great difficulty with which we are faced in discussing the question of the relation of flies to the prevalence of summer diarrhœa is that it has not been proved to the satisfaction of most investigators what the specific pathogenic organism is, or perhaps there are associated organisms. Morgan (1906-7) isolated a bacillus which he designated "No. 1," and which appears to be an important factor in the causation of the disease. In a further paper Morgan and Ledingham (1909) give a more complete account of their researches on Morgan's bacillus which belongs to the non-lactose fermenting group, to which group all the pathogenic bacteria inducing affections of the intestinal tract belong, namely, the typhoid and paratyphoid bacilli, the dysentery and food-poisoning organisms. In 1905, 58 cases of infantile diarrhœa were examined and Morgan's bacillus was found in 48·2 per cent.; in 1906, in 54 cases it was found in 55·8 per cent.; in 1907, 191 cases were examined and it occurred in 16·2 per cent., and in 1908 it occurred in 53 per cent. of the cases, numbering 166, that were examined. It was found that rats and monkeys were susceptible to infection by feeding and that they succumbed after a period of diarrhœa. One of the most interesting and highly suggestive results of the research was the discovery of Morgan's bacillus in flies. " Batches of flies came for

examination from infected and uninfected houses in Paddington and from a country house situated many miles from London, where no cases of diarrhœa had occurred, at any rate within a radius of two miles. The flies were killed with ether vapour and crushed with a sterile rod in peptone broth. The result was that Morgan's bacillus was isolated from nine of the thirty-six batches from infected houses and from one of the thirty-two batches from uninfected houses. It was also got in five out of twenty-four batches from the country house." Dr. Morgan in the course of a letter to me says: "I certainly think they are carriers of summer diarrhœa, and the variety I especially suspect of doing this is the *Musca domestica*."

Hamer in his first report (1908) points out a difficulty in the way of accepting this relation of flies to summer diarrhœa. He states: "It should be pointed out that there are certain difficulties in the way of accepting the thesis that the correspondence exhibited in the curves [he refers to the fly curve and diarrhœa curve] affords reason for concluding that flies and summer diarrhœa stand to one another in relation of cause and effect. At the commencement of the hot summer weeks, when the number of flies has begun to show marked increase, the diarrhœa curve is rapidly rising. After some weeks the number of flies reaches the maximum, and then diminishes, and so, in almost precise correspondence, does the amount of diarrhœa. A period is later reached, towards the close of the hot weeks, at which the number of flies is still as markedly excessive as at the earlier period when the amount of diarrhœa was increasing, but at the later period the amount of diarrhœa is declining; it even anticipates decline in the number of flies. If the fly is to be regarded as the carrier of the organism which causes diarrhœa, it might perhaps have been anticipated that at the later period—the number of flies still being excessive and infective material being then presumably more widely

distributed than ever before—the amount of diarrhœa, instead of showing early and rapid decline, would still be increasing. It would almost appear that the advocate of the ‘fly-borne diarrhœa hypothesis’ must necessarily fall back in support of his theory upon the hypothetical organism, conveyed by the fly, which he may claim is affected by temperature in such a way as to bring about correspondence between the diarrhœa curve and the fly curve. The very closeness of the correspondence between these two curves may indeed from this point of view be thought of as constituting a difficulty rather than a point in favour of the hypothesis that *summer diarrhœa is caused by flies.*” [The italics are mine.—C. G. H.] No one, I think, would argue this. What *is* argued is that there are excellent grounds for believing that flies carry the infective organism or organisms of summer diarrhœa.

Niven (1904) suggested that the explanation of the falling off of the diarrhœa curve while the number of flies still remain large might be due to the exhaustion of susceptible material.

The one point which does not appear to be considered and which, I think, will explain this seeming objection is the great susceptibility of flies to changes of temperature, which fact all who have studied closely the habits of *M. domestica* and its allies will admit. When the temperature falls, flies become more sluggish and retire more into the shelter of houses and other buildings, although their numbers may still be considerable. It is necessary, therefore, to study the temperature curve in addition to the fly and diarrhœa curves. If this is done, it is usually found that the fall in the number of flies is preceded by a fall in the temperature and that these two curves are associated closely, that is, the numerical activity of the flies—since the numbers caught are more indicative of their numerical *activity* than of their numerical occurrence—is dependent upon the temperature.

and also, I have found, on the state of the weather and sky. If the flies therefore become less active, they will be less liable to transmit the organisms causing summer diarrhœa, and although the numbers caught in the houses may exceed in numbers those caught earlier in the season when the diarrhœa curve was rising, those which are very active will be less in number and consequently instead of increasing, the diarrhœa curve begins to fall. The dissemination of summer diarrhœa is brought about chiefly owing to the activity of the flies outside the houses as well as inside. A fall in temperature or a spell of dull weather decreases considerably this outside activity and will therefore cause a decline in the number of diarrhœa cases. The number of cases of diarrhœa is dependent on the *activity* of the flies, and this is dependent on climatic conditions, chief of which is temperature. Considered in the light of these facts this seeming difficulty is not an argument against the idea that we hold on the relation of flies to summer diarrhœa, but rather one in support of it.

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## II. BACTERIA AND FUNGAL SPORES CARRIED BY *MUSCA DOMESTICA*.

In the summer of 1908 my friend Mr. H. T. Güssow, Dominion Botanist of Canada, made three extremely interesting and instructive experiments with a view to discovering the kinds of organisms which the house-fly may normally carry, and he has kindly allowed me to give his results, hitherto unpublished, here.

### *Experiment No. 1.*

A fly was caught in his living room (Norwood, London) at 10 a.m. on May 4th and allowed to walk over nutrient agar-agar in a Petri dish; the necessary precautions being taken to prevent extraneous infection of the medium. The

Petri dish was placed in an incubator and kept at 28°—30°C. At 6 p.m. on the same day there were plain indications of colonies forming but they were too small to allow a separation count.

May 5th, 10 a.m.—7 colonies of Bacteria and 4 of Fungi showing.

„ 6th, 10 a.m.—16 colonies of Bacteria and 5 of Fungi showing.

„ 7th, 10 a.m.—23 colonies of Bacteria and 6 of Fungi showing.

„ 8th, 10 a.m.—30 colonies of Bacteria and 6 of Fungi showing.

• That is, in 96 hours, 30 colonies of Bacteria and 6 colonies of Fungi were observed.

The fungi were examined and identified as follows:—

2 colonies of	<i>Saccharomyces</i> sp.
2 „ „	<i>Penicillium glaucum</i> .
1 colony „	<i>Aspergillus niger</i> .
1 „ „	<i>Cladosporium herbarum</i> .

The bacteria were removed in the ordinary manner and were sub-cultured, plated out and identified as follows:—

<i>Micrococcus ureae</i>	... ..	2 colonies.
<i>Bacillus subtilis</i>	... ..	7 „
<i>Bacillus coli commune</i>	... ..	11 „
<i>Sarcina lutea</i>	... ..	2 „
Stained by Gram...	... ..	3 „
Not stained by Gram	... ..	5 „

### *Experiment No. 2.*

A fly was caught at 11.30 a.m. on May 4th out of doors on Central Hill, Norwood, London, and was allowed to walk over nutrient agar-agar at 12 o'clock noon.



- May 4th, 6 p.m.—Colonies were plainly forming.  
 ,, 5th, 10 a.m.—13 colonies of Bacteria and 6 colonies of Fungi.  
 ,, 6th, 10 a.m.—21 colonies of Bacteria and 7 colonies of Fungi.  
 ,, 7th, 10 a.m.—39 colonies of Bacteria and 7 colonies of Fungi.  
 ,, 8th, 10 a.m.—46 colonies of Bacteria and 7 colonies of Fungi.

That is, in 94 hours, 46 colonies of Bacteria and 7 colonies of Fungi were obtained from this fly No. 2. The fungi were identified as follows:—

- 2 colonies of *Macrosporium* sp.  
 3 ,, ,, *Penicillium glaucum*.  
 1 colony ,, *Cladosporium herbarum*.  
 1 ,, ,, *Fusarium roseum*.

The bacteria after being sub-cultured and plated out were identified as:—

<i>Bacillus tumescens</i>	... ..	18 colonies.
<i>Micrococcus pyogenes aureus</i>	9	,,
<i>Sarcina lutea</i>	... ..	2
<i>Sarcina ventriculi</i>	... ..	1 colony.
<i>Bacillus amylobacter</i>	... ..	4 colonies.
Acid fast bacillus...	... ..	1 colony.
Stained by gram	... ..	4 colonies.
Not stained by gram	... ..	7

### *Experiment No. 3.*

This experiment was perhaps the most interesting of the three as the fly was captured at 10.30 a.m. on May 4th on a dust bin (Norwood, London), a situation in which flies are frequently found. It was allowed to walk over the surface of nutrient agar-agar.

May 4th, 6 p.m.—Signs of colonies observed.

„ 5th, 10 a.m.—18 colonies of Bacteria and 7 colonies of Fungi.

„ 6th, 10 a.m.—58 colonies of Bacteria and 9 colonies of Fungi.

„ 7th, 10 a.m.—113 colonies of Bacteria and 10 colonies of Fungi.

„ 8th, 10 a.m.—116 colonies of Bacteria and 10 colonies of Fungi.

That is, after  $95\frac{1}{2}$  hours, 116 colonies of Bacteria and 10 colonies of Fungi were obtained from this single fly. The fungi were identified as:—

<i>Penicillium glaucum</i> ... ..	4 colonies.
<i>Eurotium</i> sp. ... ..	1 colony.
<i>Saccharomyces</i> sp. ... ..	2 colonies.
<i>Fusarium roseum</i> ... ..	1 colony.
<i>Aspergillus niger</i> ... ..	1 „
<i>Mucor racemosa</i> ... ..	1 „

The bacteria after having been sub-cultured and plated out were identified as:—

<i>Bacillus coli commune</i> ...	34 colonies.
<i>Bacillus subtilis</i> ... ..	16 „
<i>Bacillus tumescens</i> ... ..	8 „
<i>Bacillus lactis acidii</i> ... ..	4 „
<i>Sarcina lutea</i> ... ..	12 „
<i>Sarcina ventriculi</i> ... ..	2 „
<i>Micrococcus pyogenes aureus</i>	21 „
<i>Micrococcus ureæ</i> ... ..	11 „
Acid fast bacilli ... ..	2 „
Bacilli stained by gram ...	4 „
Bacilli not stained by gram	2 „

The extremely large number and preponderance of bacilli carried by this fly No. 3 shows very strikingly the infection which a fly frequenting such miscellaneous household refuse as is contained in the average household dustbin and the results of such careful experiments as those which are recorded above demonstrate clearly not only that flies normally carry about the spores of fungi and bacteria and the extra-infection which they obtain by frequenting refuse, but also their liability to carry and disseminate such bacteria, pathogenic and non-pathogenic, with which they may come into contact in their wanderings. Such a demonstration as to their ability to transfer non-pathogenic, putrefactive, or pathogenic organisms renders further comment unnecessary.

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### III. FLIES AND MILK.

An instructive example of the influence of flies and milk in the dissemination of typhoid fever is communicated by Taylor (Colorado State Board of Health, U.S.A.) to the New York Merchants' Association. He says: "In the city of Denver we had a very sad as well as a plain demonstration of the transmission of typhoid fever by flies and milk. Early in August of this year the wife of a dairyman was taken with typhoid fever, remaining at home about three weeks before her removal to the hospital, August 28th. During the first two weeks in September we received reports of numerous cases of typhoid fever in the northern portion of Denver, and upon investigation found that all these cases had been securing their milk from this dairy. An inspection of the dairy was then made, and in addition to learning of the illness of the dairyman's wife, we also found the dairyman himself suffering with a mild case of typhoid fever, but still up and delivering milk. The water supply of this dairy was fairly good. However, we found that the stools of

both the wife and husband had been deposited in an open privy vault located thirty-five feet from the milk-house, which was unscreened and open to flies. The gelatine culture exposed for thirty minutes in the rear of the privy vault and in the milk-house among the milk-cans gave numerous colonies of typhoid bacilli, as well as colon bacilli and the ordinary germ-life. The source of infection in the dairyman's wife's case is unknown, but I am positive that in all the cases that occurred on this milk route the infection was due to bacilli carried from this vault by flies and deposited upon the milk-cans, separator and utensils in the milk-house, thereby contaminating the milk. The dairyman supplied milk to 143 customers. Fifty-five cases of typhoid fever occurred, and six deaths resulted therefrom." (From "The House-fly at the Bar Indictment Guilty or Not Guilty?" The Merchants' Association of New York. April, 1909, 48 pp.)

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#### IV. FLIES IN MILITARY CAMPS.

Dutton (1909) gives an interesting figure to demonstrate the manner in which flies would be carried from sources of typhoid infection (Division Hospitals and Latrines) in the Camps of the United States Army at Fernandina and Tampa to different parts of these camps. He states that Sergeant Brady, who was stricken with typhoid fever at Fernandina, mentioned to him that the lime used about the latrines and garbage dumps was carried by flies to the food which was being used in the camps.

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#### XIV. APPENDIX B.

##### ADDITIONAL OBSERVATIONS ON THE BREEDING HABITS OF *MUSCA DOMESTICA*.

Since the third part of this monograph was written and sent to press (July, 1908) I have collected further data as to

the substances in which they are able to breed, and to make this account of the bionomics of *Musca domestica* as complete as possible I am giving a brief account of them here.

In the collection of Diptera in the Division of Entomology of the Department of Agriculture of Canada, I found specimens of *M. domestica* which had been reared in germinating wheat. The parent fly had no doubt chosen such material as an admirable nidus for her progeny, as germinating wheat, on account of the fermentation taking place in the same, forms an excellent substance for the development of the larvæ.

Allied to this observation are some experiments by Nash (1909) in which he reared flies in fermenting bread, and his methods were followed by Jepson in the experiments already recorded. Nash also mentions (*l.c.*) that he has succeeded in rearing them on pear, potato, banana skins, boiled rice and old paper, but he experienced the same failure as I did in attempting to breed them in cheese. He records an interesting observation of Austen's which the latter made in 1908. Austen found the larvæ of *M. domestica* in rubber which was suspended in a drying room at a temperature of 100°F. They were apparently full grown and the circumstances indicated that they could not have been more than three days in developing from the egg stage, which indicated a rapid growth at this exceedingly high temperature.

The foregoing observations taken in conjunction with those of my own and other investigators given in the second part of this monograph emphasise the fact that *M. domestica* is able to breed in practically any decaying animal or vegetable substance or excrement, especially if it is in a state of fermentation and if there is a sufficient amount of moisture and a suitable temperature, the last two conditions being concomitant with fermentation.

## XV. APPENDIX C. PREVENTIVE MEASURES.

In 1897 Howard conducted a series of experiments with a view to discovering an insecticidal substance which could be used for the destruction of the larvæ in the heaps of manure in which they were breeding. He found that both lime and gas lime were not efficacious. In an experiment in which 8 lbs. of horse manure containing larvæ were treated with a pint of kerosene, which was washed down into the manure with water, it was found that all the larvæ were killed. He also found that by treating 8 lbs. of well-infested horse manure with one pound of chloride of lime all the larvæ were killed, but the results were not satisfactory when a quarter of the quantity of chloride of lime was used. On experimenting with the kerosene treatment on a large scale he found that it was not only laborious but also not entirely successful, as is sometimes the case in the practical application on a large scale of successful experimental methods. He therefore devised another method of treating the horse manure of stables. A chamber six feet by eight feet was built in the corner of the stable with which it communicated by means of a door; it was provided also with a window furnished with a wire screen. The manure was thrown into the chamber every morning and a small shovelful of chloride of lime scattered over it. At the end of ten days or a fortnight the manure was removed through an open door and carted away. The experiment was carried out in the stable of the U.S. Department of Agriculture and a marked decrease in the number of flies was observed.

In France residuum oil has been proposed as a suitable substance for the destruction of the eggs and larvæ in privies and cesspools. Of such insecticidal substances as have been practically tested chloride of lime is undoubtedly the cheapest and most efficacious. The best preventive measure, however,



which can be suggested as a result of the study of the breeding habits is the periodical and regular removal of the horse-manure at intervals not exceeding seven days. The use of insecticidal substances could not be satisfactorily supervised, apart from the fact that there would be a great risk of their not being wholly efficacious. The periodic removal of the breeding places could be regulated. The same method of procedure should also be adopted with respect to the other breeding places such as kitchen refuse, the keeping of which in perfectly closed receptacles should be enforced as also the periodic emptying of the same within seven days in the summer months. The substitution of modern methods of water-carriage for the older conservancy methods in privies, etc., will abolish a very common breeding place and also a common source of infection. The destruction of refuse by public and other destructors instead of its deposition on 'tips' would decrease a common breeding place. In a few words, the prohibition of the exposure and the frequent periodic removal of the substances in which *Musca domestica* has been shown to breed are the methods to be employed to bring about its numerical reduction and a diminution of its liability to bacterial infection.

In addition, such substances as milk, sugar, etc., to which flies are attracted, should be kept covered, and flies should not be allowed to come into contact with any food substances nor with the faces of young children or persons who are ill but should be prevented from doing so by means of muslin or other screens.

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#### XVI. APPENDIX D.

##### A FURTHER PARASITE OF THE HOUSE-FLY (*MUSCA DOMESTICA*).

In a series of papers, of which the first only has appeared, Girault and Sanders (1909) are describing a number of

hymenopterous parasites reared from *Musca domestica*. All the parasites belong to the family Pteromalidae and the three generic forms which predominated were *Spalangia*, Latreille; *Muscidifurax*, Girault and Sanders; and *Nasonia*, Ashmead. One species of the last genus only is described in the first paper of the series, namely, *Nasonia brevicornis*, Ashmead.

*Nasonia brevicornis*, Ashmead.

It was found that this small parasite which is very sluggish in its movements attacked the larvæ and pupæ of *Musca domestica* in confinement. A number of males and females were reared from the pupæ of *M. domestica*. The female of *N. brevicornis* varies in length from 1 mm. to 2·30 mm., and is of a metallic dark brassy green colour, the eyes are garnet. The male is about one-third smaller than the female, varying in length from 0·60 mm. to 2·00 mm. It is lighter in colour, more brassy in appearance, metallic and green; the eyes are sometimes a brilliant carmine.

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#### ERRATA.

- P. 3, read *Berlese* for *Belese*.  
P. 21, read *macrochaetae* for *macrochaebae*.  
P. 154, read *Haematopota* for *Haemalopota*.

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